AN ECOLOGICAL-PHYSIOLOGY PERSPECTIVE ON SEABIRD RESPONSES TO CONTEMPORARY AND HISTORIC ENVIRONMENTAL CHANGE

By

Alexis P. Will

A Dissertation Submitted in Partial Fulfillment

for the Degree of

Doctor of Philosophy

in

Biological Sciences

University of Alaska Fairbanks

May 2017

APPROVED:

Alexander Kitaysky, Committee Chair
Greg Breed, Committee Member
Abby Powell, Committee Member
Alan Springer, Committee Member
Kris Hundertmark, Chair
Department of Biology and Wildlife
Paul Layer, Dean
College of Natural Science and Mathematics
Michael Castellini, *Dean of the Graduate School*

Abstract

The chapters included in this dissertation implement an ecological-physiology approach to understanding how long-lived marine organisms, using seabirds as a model, respond to changes in the environment. Many seabird populations are governed by bottom-up processes, yet efforts to connect prey dynamics and parameters such as breeding performance often yield mixed results. Here I examined how individual foraging behavior and nutritional status change at the inter-annual, decadal, and multi-decadal scale. I validated that the concentration of the avian stress hormone in seabird feathers is indicative of their exposure to nutritional stress. I then used this technique to show that young seabirds (rhinoceros auklets, *Cerorhinca monocerata*) that experience variable foraging conditions during their prolonged nestling period incurred higher nutritional stress when provisioned with prey that was relatively low in energy content. On the other hand, when examining adult foraging behavior, a signal of environmental variability was lost in the noise of changing diets. Foraging behavior of adults appeared to be highly flexible and less informative in regard to detecting an environmental change. I used stable isotope analysis to re-construct the isotopic niche dynamics (where and at what trophic level seabirds were obtaining prey) and partitioning of food resources for three abundant seabirds (common and thick-billed murres, *Uria aalge,* and *U. lomvia,* respectively; and black-legged kittiwakes, *Rissa tridactyla*) breeding in the southeastern Bering Sea under cold and warm states of the ecosystem. Access to diverse habitat reversed how seabirds partitioned prey during food shortages: seabirds with access to multiple habitats contracted their isotopic niche during food-limited conditions in contrast to the expansion of the isotopic niche observed for seabirds with access to only one type of habitat. Finally, I measured nutritional stress and stable isotope signatures (carbon and nitrogen) in contemporary and historic red-legged kittiwake (*Rissa brevirostris*) feather samples to examine how birds breeding on St. George Island have responded to changes in summer and winter conditions in the Bering Sea over time. Red-legged kittiwakes were less nutritionally stressed during warm summers and winters. It is not clear, however, whether all seabirds would do well if the Bering Sea were to break with its pattern of oscillating between warm and cold conditions. Prey for these birds may either be negatively affected by continuously warm conditions (murres and black-legged kittiwakes feeding on juvenile pollock, *Gadus chalcogrammus*) or the conditions that are most beneficial to the prey are not known (red-legged kittiwakes feeding on myctophids). With this work I suggest that measuring nutritional stress in feathers and using stable isotope analysis to characterize foraging niches may document more dynamic responses to changes in the environment than population level parameters such as breeding performance. To do so, however, requires a better understanding of the relationship between these individual-level responses and fitness.

Table of Contents

List of Figures

Page

List of Tables

Page

List of Appendices

Acknowledgements

This body of work would not be possible without the support, encouragement, and a huge time investment from more people than I have room to thank. There are a few that stand out from the rest. Thank you first to my advisor, Sasha, for all the time and effort you've invested in me, and to my committee members for helping to pull each of these chapters together. Thank you to Zhenya for your advice and perspective on what it means to be a good human, and to Leslie Slater and Jan Straley for starting me (as well as many other women) on this path of science. To my mom, you are a source of endless support, and a role model for what it means to have strength and persevere. I know I would never have been this successful without you as a cheerleader. Elliot. Thank you for all the dinners, the dog walks, the magical events, the adventures, and for taking each new addition to our life in stride. For example, Kronos! Pants, you've been a challenge, but you also get me outside every day and I can't help but enjoy your enthusiasm for everything, even squirrels. To all my friends and family, if I tried to list you all I would invariably leave someone important out. Thank you for being there through all the times and believing in me. If ever I think I can't do something there is always someone quick to remind me that I can.

General Introduction

Understanding how individual long-lived animals respond to environmental variability can lend insight into population dynamics, and provide wildlife managers with a better understanding of how future changes in the environment may or may not affect a particular species. Understanding such responses of animals can also lend insight into how the structure of their food web may be changing. In the marine environment, where many members of the food web are difficult for researchers to access and observe, seabirds offer an approach to understanding how environmental change affects marine ecosystems that circumvents some of the difficulties faced by marine researchers (Burger and Shaffer 2008). Their reproductive output and populations are readily available to sample, and measures of diet and physiological state are relatively easy to obtain. Some species are widespread and many offer opportunities to test ecological and evolutionary principles in long-lived, free-living organisms (e.g., Brommer et al. 2008). Many species are sensitive to local environmental change and may exhibit responses to climate change before signals are detected in more regional-scale data, such as climate indices, or fisheries surveys (e.g., Wolf et al. 2010). For example, some seabirds track forage fish species of commercial interest through their diets, breeding performance, and population trends, and may be useful to fisheries managers (e.g., Wanless et al. 2007).

Variability in the environment helps to shape the morphology, physiology, behavior, and life-history strategy of animals. In recent decades rapid climate change has resulted in increased environmental variability and extreme weather events that may affect the distribution and survival of organisms (Parmesan 2006, McKenney et al. 2007, Møller et al. 2011, Carey 2014). Long-lived species such as seabirds (15-30 years), inhabiting environments characterized by short-term variability, may provide insight into the coping mechanisms of organisms to withstand high frequency environmental variation. Organisms that have adapted to such dynamic environments have strategies to determine when to invest energy in self-maintenance or in reproduction (Stearns 1977). For example, species that inhabit both the Atlantic and Pacific oceans show different life history strategies: individuals living in the comparatively stable Atlantic Ocean reproduce at younger ages, are more persistent in their reproductive attempts, and have shorter lifespans than their Pacific-dwelling counterparts (Suryan et al. 2009, Schultner et al. 2013).

Seabird responses to environmental variability may be measured at the demographic level as reproductive output, fledging success, juvenile recruitment, adult survival, and/or population trends. There has been some success in finding relationships between environmental indices and seabird population parameters (Sandvik et al. 2005), but matching the time-scale of the seabird parameters to climate can be difficult. In the Bering Sea, murre (*Uria spp.*) and kittiwake (*Rissa spp.*) reproductive performance was found to be correlated to environmental indices when they were examined within

climate regimes (Springer 1998), lagged (Zador et al. 2013), or not at all (Renner et al. 2014). On a broad spatial scale correlations to environmental indices may break down, with colonies responding to regional indices quite differently (Satterthwaite et al. 2012, Murphy et al. 2016), making it difficult to draw any definitive conclusions. In addition, it is not always clear to what degree carry-over effects may influence responses. That is, when the conditions or experiences met in one season affect the reproduction or survival of an individual in the following season (Harrison et al. 2011, Schultner et al. 2014). Changes in environmental conditions may occur over different periods of time: multi-decadal, decadal, inter-annually, or seasonally. The mixed success in matching seabird reproduction to environmental indices may be due in part to a mismatch between the measured response and the time scale of the environmental variability, or because the environment affects foraging behavior more than reproduction (e.g., Einoder et al. 2013).

Another approach is to compare seabird population processes to food availability, since these parameters are often, but not always, driven by bottom-up processes dictated by the environmental conditions prey experience (Einoder 2009). Seabird responses to environmental change, i.e., food availability, can be examined by comparing population processes and changes in individual condition relative to prey availability or climate indices (e.g., population and prey, Oro et al. 2004; individual condition and climate, Satterthwaite et al. 2012). Forging a link between seabirds and their food is, however, not entirely straightforward. Exploring predator-prey relations can be informative (Erikstad et al. 2013, Santoro et al. 2014), but an in-depth understanding requires intensive sampling of the marine environment for prey species and a comprehensive understanding of the diet utilized by birds foraging in that area. Furthermore, some caution must be employed prior to examining predator-prey relationships because not all seabird populations are regulated by only bottom-up processes (e.g. Reilly et al. 2013). An alternative approach may be to characterize the habitat and trophic level that make up the foraging niche of a single, or group, of seabird species. By using a less detailed, but easy to obtain, measure of diet (stable isotope analysis) it may be possible to construct an isotopic niche and examine how the niche changes in response to changes in the environment (e.g., Moreno et al. 2016). Isotopic niches are most commonly built using carbon and nitrogen stable isotope ratios to characterize where (nearshore or pelagic) and at what trophic level the prey an organism consumes is located (Bearhop et al. 2004).

Physiological parameters have also been used to understand responses to environmental conditions at both the individual and population level. General strategies for dealing with environmental variability may be discerned by measuring the rate of telomere loss, a metric of biological age, which may indicate the pace at which an individual is living (slow or fast, Haussmann et al. 2003). Other measures have been used to assess energy stores (triglycerides), the state of the immune system (leucocyte counts), and metabolic efficiency (protein content). In seabirds, the stress hormone corticosterone (CORT) has

been demonstrated to provide insight into the foraging conditions individuals encounter (e.g., Barrett et al. 2015). CORT is a glucocorticoid produced by the adrenals and regulated by the hypothalamus and pituitary gland. Glucocorticoids influence energy mobilization, resource allocation, immune response, reproduction, and growth (Breuner et al. 2013). It has been shown for multiple species of seabirds that the life-stage independent upregulation of the hypothalamus-pituitary-adrenal response is largely initiated by limitations on food intake, whether from food shortages or decreases in food quality (e.g., Kitaysky et al. 2001, Kitaysky et al. 2007, Benowitz-Fredericks et al. 2008, Doody et al. 2008, Harding et al. 2013). Thus, relative concentrations of circulating baseline CORT can be used as a proxy for food availability (Kitaysky et al. 2010) and have been demonstrated to impact fitness (e.g., Satterthwaite et al. 2010).

Until recently, measuring CORT concentration in seabirds has been somewhat limited by the type of tissue sampled for analysis. CORT has most often been measured in blood plasma, but also in guano. Plasma provides a snapshot of the status of a bird at the time of sampling. While guano provides a somewhat more integrated measure of the experience of a bird over several hours, both methods are limited in their ability to profile an individual's experience, and thus foraging conditions, over a longer time period (Brewer et al. 2008). These measures are also limited to periods when birds are accessible to catch or in places where it is possible to collect fresh droppings. In contrast, it has been demonstrated that CORT can be measured in feather tissues (Bortolotti et al. 2008) and that it remains stable through time (Bortolotti et al. 2009). This creates the possibility to measure the nutritional state of a seabird during the non-breeding life period and compare current nutritional states with historical ones to determine how conditions may have changed over time. Whether this technique also provides a proxy for food availability in seabirds, however, is not well understood.

In this dissertation, I experimentally validate the use of feather CORT as a measure of nutritional stress incurred by seabirds (Chapter 1). I also explore the use of feather CORT (Chapter 2, 4) and stable isotope analysis (Chapter 3, 4) to measure the response of seabirds to environmental variability at four different time scales: seasonal (Chapter 2, 3), inter-annual (Chapter 2), decadal (Chapter 3), and multi-decadal (Chapter 4). In so doing I tested new approaches to measuring seabird responses to environmental change, and assessed their usefulness. In addition I produced some of the first decadal (Chapter 3), multi-decadal (Chapter 4) and annual (capturing the annual cycle - Chapter 4) analyses of how seabirds respond to climate variability during a period when the effects of climate change are increasingly apparent worldwide (Walther et al. 2002).

References:

Barrett RT, Erikstad KE, Sandvik H, Myksvoll M, Jenni-Eiermann S, Kristensen DL, Moum T, Reiertsen TK, Vikebø F. (2015). The stress hormone corticosterone in a marine top predator reflects short-term changes in food availability. *Ecology and Evolution*. 5:1306-1317.

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H. (2004). Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology*. 73:1007-1012.

Benowitz-Fredericks ZM, MT Shultz, AS Kitaysky. (2008). Stress hormones suggest opposite trends in food availability for planktivorous and piscivorous seabirds in 2 years. *Deep-Sea Research II*. 55:1868-1876.

Bortolotti GR, Marchant T, Blas J, Cabezas S (2009) Tracking stress: localisation, deposition and stability of corticosterone in feathers. The Journal of experimental biology 212:1477-1482

Bortolotti GR, Marchant TA, Blas J, German T (2008) Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. Functional Ecology 22:494-500

Breuner CW, Delehanty B, Boonstra R. (2013). Evaluating stress in natural populations of vertebrates: total CORT is not good enough. *Functional Ecology*. 27:24-36.

Brewer, JH, O'Reilly, K.M., Kildaw, S.D. and Buck, C.L. (2008). Interannual variation in the adrenal responsiveness of black-legged kittiwake chicks (*Rissa tridactyla*). *General Comparative Endocrinololgy* 156, 361-368.

Brommer JE, Rattiste K, Wilson AJ. (2008). Exploring plasticity in the wild: laying date-temperature reaction norms in the common gull *Larus canus*. *Proceedings of the Royal Society B*. 275:687-693.

Burger AE, Shaffer SA. (2008). Application of tracking and data-logging technology in research and conservation of seabirds. *The Auk*. 125:253-264.

Carey C. (2014). Climate change, extinction risks, and reproduction of terrestrial vertebrates. Holt WV, Brown JL, Comizzoli P (eds). *Reproductive Sciences in Animal Conservation*. Springer. New York NY. pp 35-54.

Doody LM, Wilhelm SI, McKay DW, Walksh CJ, Storey AE. (2008). The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. *Hormones and Behavior* 53:140-148.

Einoder LD. (2009). A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* 95:6-13.

Einoder LD, Page B, Goldsworthy SD. (2013). Feeding strategies of the short-tailed shearwater vary by year and sea-surface temperature but do not affect breeding success. *The Condor*. 115:777-787.

Erikstad KE, Reiertsen TK, Barrett RT, Vikebø F, Sandvik H. (2013). Seabird–fish interactions: the fall and rise of a common guillemot *Uria aalge* population. *Marine Ecology Progress Series.* 475:267-276.

Harding A, Parades R, Suryan R, Roby D, Irons D, Orben R, Renner H, Young R, Barger C, Dorresteijn I, Kitaysky A. (2013). Does location really matter? An inter-colony comparison of thick-billed murres (Uria lomvia) breeding at varying distances to productive oceanographic features in the Bering Sea. *Deep-Sea Research II.* 94:178-191.

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. (2011). Carry-over effects as drivers of fitness differences in animals. *Jounral of Animal Ecology.* 80:4-18.

Haussmann MF, Winkler DW, O'Reilly KM, Huntington CE, Nisbet ICT, Vleck CM. (2003). Telomeres shorten more slowly in long-lived birds and mammals than in short-lived ones. *Proceedings of the Royal Society B.* 270:1387-1392.

Kitaysky, A.S., Kitaiskaia, E.V., Wingfield, J.C. and Piatt, J.F. (2001). Dietary Restriction Causes Chronic Elevation of Corticosterone and Enhances Stress Response in Red-legged Kittiwake Chicks. *J Comp. Physiol. B* 171, 701-709.

Kitaysky, A.S., Piatt, J.F. and Wingfield, J.C. (2007). Stress Hormones Link Food Availability and Population Processes in Seabirds. *Mar. Ecol-Prog. Ser.* 352, 245-258.

Kitaysky, A.S., Piatt, J.F., Hatch, S.A., Kitaiskaia, E.V., Benowitz-Fredericks, Z.M., Shultz, M.T. and Wingfield, J.C. (2010). Food Availability and Population Processes: Severity of Nutritional Stress During Reproduction Predicts Survival of Long-lived Seabirds. *Funct. Ecol.* 24, 625-637.

McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF. (2007). Potential impacts of climate change on the distribution of North American trees. *BioScience*. 57:939-948.

Møller AP, Wolfgang F, Berthold P (eds). (2011). *Effects of Climate Change on Birds*. Oxford University Press. New York, NY.

Moreno R, Stowasser G, McGill RAR, Bearhop S, Phillips RA. (2016). Assessing the structure and temporal dynamics of seabird communities: the challenge of capturing marine ecosystem complexity. *Journal of Animal Ecology.* 85:199-212.

Murphy EC, Roseneau DG, Springer AM, Byrd GV. (2016). Breeding chronology and productivity of black-legged kittiwakes *Rissa tridactyla* at Bluff, Alaska, 1975-2008: associations with regional environmental indices and distant colonies. *Marine Ornithology*. 44:183-201.

Oro D, Cam E, Pradel R, Martínez-Abraín A. (2004). Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proceedings of the Royal Society B*. 271:387-396.

Parmesan C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review in Ecology, Evolution, and Systematics.* 37:637-669.

Reilly TOM, Fraser HM, Fryer RJ, Clarke J, Greenstreet SPR. (2013). Interpreting variation in fish-based food web indicators: the importance of "bottom-up limitation" and "top-down control" processes. *ICES Journal of Marine Science.* 71(2):406-416.

Renner HM, Drummond BA, Benson A-M, Paredes R. (2014). Reproductive success of kittiwakes and murres in sequential stages of the nesting period: Relationships with diet and oceanography. *Deep-Sea Research II.* 109:251-265.

Sandvik H, Erikstad KE, Barrett RT, Yoccoz NG. (2005). The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology.* 74:817–831.

Santoro JA, Schroeder ID, Field JC, Wells BK, Sydeman WJ. (2014). Spatio-temporal dynamics of ocean conditions and forage taxa reveals regional structuring of seabird-prey relationships. *Ecological Applications.* 24:1730-1747.

Satterthwaite WH, Hatch SA, Piatt JF, Kitaysky AS, Mangel M. (2010). Unifying quantitative life-history theory and field endocrinology to assess prudent parenthood in a long-lived seabird. *Evolutionary Ecology Research*. 12:779–792.

Satterthwaite WH, Kitaysky AS, Mangel M. (2012). Linking climate variability, productivity and stress to demography in a long-lived seabird. *Marine Ecology Progress Series.* 454:221-235

Schultner J, Kitaysky AS, Gabrielsen GW, Hatch SA, Bech C. (2013). Differential reproductive responses to stress reveal life-history strategies within a species. *Proceedings of the Royal Society B.* 280:20132090.

Schultner J, Moe B, Chastel O, Tartu S, Bech C, Kitasyky AS. (2014). Corticosterone mediates carry-over effects between breeding and migration in the kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series.* 496:125-133.

Springer AM. (1998). Is it all climate change? Why marine bird and mammal populations fluctuate in the North Pacific. In: G. Halloway, P. Muller, and D. Henderson (eds) *Biotic impacts of extratropical climate change in the Pacific*. University of Hawaii:109-119.

Stearns SC. (1977). The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics*. 8:145-171.

Suryan RM, Saba VS, Wallace BP, Hatch SA, Frederiksen M, Wanless S. (2009). Environmental forcing on life history strategies: Evidence for multi-trophic level responses at ocean basin scales. *Progress in Oceanography*. 81:214-222.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F. (2002). Ecological responses to recent climate change. *Nature*. 416:389-395.

Wanless S, Frederiksen M, Daunt F, Scott BE, Harris MP. (2007). Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. *Progress in Oceanography*. 72:30-38.

Wolf SG, Snyder MA, Sydeman W, Doak D, Croll DA. (2010). Predicting population consequences of ocean climate change for an ecosystem sentinel, the seabird Cassin's auklet. *Global Change Biology.* 16:1923-1935

Zador S, Hunt Jr. GL, TenBrink T, Aydin K. (2013). Combined seabird indices show lagged relationships between environmental conditions and breeding activity. *Marine Ecology Progress Series.* 485:245–258.

Chapter 1 Feather Corticosterone Reveals Developmental Stress in Seabirds[1]

Abstract

In nest-bound avian offspring, food shortages typically trigger a release of the stress hormone corticosterone (CORT). Recent studies indicate that CORT is passively deposited in the tissue of growing feathers and thus may provide an integrated measure of stress incurred during development in the nest. The current hypothesis predicts that, assuming a constant rate of feather growth, elevated CORT circulating in the blood corresponds to higher levels of CORT in feather tissue, but experimental evidence for nutritionally stressed chicks is lacking. Here, we examined how food limitation affects feather CORT content in the rhinoceros auklet (*Cerorhinca monocerata*). We (1) used captive chicks reared on control versus restricted diets, and (2) applied this technique to free-living chicks with unknown nutritional histories that fledged at three separate colonies. We found that (1) feather growth was not affected by experimentally induced nutritional stress; (2) captive chicks raised on a restricted diet had higher levels of CORT in their primary feathers; (3) feather CORT deposition is a sensitive method of detecting nutritional stress; and (4) free-living fledglings from the colony with poor reproductive performance had higher CORT in their primary feathers. We conclude that feather CORT is a sensitive integrated measure revealing the temporal dynamics of food limitations experienced by rhinoceros auklet nestlings. The use of feather CORT may be a powerful endocrine tool in ecological and evolutionary studies of bird species with similar preferential allocation of limited resources to feather development.

[1] Will, Alexis; Suzuki, Yuya; Elliott, Kyle; Hatch, Scott; Watanuki, Yutaka; Kitaysky, Alexander. Journal of Experimental Biology. 2014. vol 217: 2371-2376, doi:10.1242/job.098533.

Introduction

The environmental stressors that animals experience during development have fitness consequences. A disruption in homeostasis in birds triggers release of the stress hormone corticosterone (CORT), which enables an individual to cope with changes in its environment (Schoech et al., 2011). For example, nutritional limitation in nestlings has been shown to increase CORT secretion (Astheimer et al., 1992; Kitaysky et al., 1999; Kitaysky et al., 2001; Pravosudov and Kitaysky, 2006; Herring et al., 2011), which in turn may increase begging behavior (Kitaysky et al., 2001), and result in a stronger adrenocortical response to future stressors (Pravosudov and Kitaysky, 2006; Spencer et al., 2009; reviewed in Schoech et al., 2011). Short- and long-term exposure to elevated CORT, however, can reduce an individual's quality (Kitaysky et al., 2003; Dehnhard et al., 2011), lower survival (Kitaysky et al., 2007; Blas et al., 2007: Kitaysky et al., 2010, Satterthwaite et al., 2010; Goutte et al., 2010) and interfere with morphological development (Müller et al., 2009; Honarmand et al., 2010). Because of the short-term benefits and long-term costs of increased CORT secretion, quantifying an individual's exposure to CORT is an informative method of assessing an individual's response to its environment (e.g. Dorresteijn et al., 2012) and may provide insight into the evolution of current life-history strategies (Kitaysky et al., 2003; Satterthwaite et al., 2010, Schoech et al., 2011, Atwell et al., 2012).

Current methods of measuring CORT exposure (such as CORT concentrations in blood and fecal samples) provide a measure of CORT levels experienced by an individual at one point in time (Brewer et al., 2008; Müller et al., 2009; Herring et al., 2011). However, even repeated samples of blood or fecal material may not always capture a complete profile of stress incurred by individuals on the scale of days or weeks. For example, experimental evidence in the red-legged kittiwake (*Rissa brevirostris*) indicates that prolonged periods of food shortage may not always correspond to an increased secretion of baseline plasma CORT (Kitaysky et al., 2001). Recently, several studies have employed a technique that measures the amount of CORT contained in feather tissues, which are grown over a period of days or weeks. Several of these studies indicate that the relatively non-invasive sampling of whole feathers may provide an integrated measure of stress incurred throughout the growth of that feather (Fairhurst et al., 2013), and that feathers can be sectioned to obtain a rough profile of stress experienced during feather growth (Bortolotti et al., 2008; Bortolotti et al., 2009; Lattin et al., 2011). The current 'passive deposition' hypothesis predicts that elevated CORT in blood plasma will correspond to higher levels of CORT in feather tissue because the CORT circulating in the blood is incorporated into the feather tissues as they are being formed (although the mechanisms are still unknown) (Bortolotti et al., 2008).

The potential ecological applications of this technique are broad and already the few published studies that employ it address questions ranging from the impact of the pre-breeding body condition on egg production (Kouwenberg et al., 2013) to the effect environmental enrichment has on the physiological

state of captive passerines (Fairhurst et al., 2011). There is evidence, however, that during development variations in resource allocation may produce feather CORT results opposite to those expected from plasma CORT studies (Patterson et al., 2014). Several validation studies have found that feather CORT concentration not only reflects the length of a feather, as originally proposed by Bortolotti et al., 2008, but also correlates significantly with a feather's mass and growth rate (Lattin et al., 2011; Patterson et al., 2014). There is a need to experimentally validate how feather growth rates and feather CORT respond to natural environmental stressors; otherwise, use of this technique may lead to equivocal interpretations of feather CORT results. To date, only a few studies have assessed the technique of measuring CORT in feather tissues of chicks that have experienced experimentally induced stressful conditions during development (Fairhurst et al., 2012b; Fairhurst et al., 2013).

We used seabirds as a model system to investigate the use of feather CORT as an indication of a chick's exposure to nutritional stress during development. In seabirds, increased CORT secretion is associated with low food availability (Doody et al., 2008; Kitaysky et al., 2007; Kitaysky et al., 2010; Dorresteijn et al., 2012) and in many species plasma CORT correlates inversely with population parameters such as reproductive success, survival, and population trends (Buck et al., 2007; Kitaysky et al., 2007, Kitaysky et al., 2010; Harding et al., 2011; Dorresteijn et al., 2012; Satterthwaite et al., 2012). Chicks experience food limitation when their parents are unable or unwilling to compensate for food shortages (Harding et al., 2009; Fairhurst et al., 2012a; Jacobs et al., 2013), thus presenting a direct physiological response of individuals to changes in their nutritional environment.

We tested the effect of nutritional stress on deposition of CORT in feathers of the rhinoceros auklet, *Cerorhinca monocerata* (Pallas 1811). Experimental and observational studies indicate that in this species chicks preferentially allocate limited resources to wing and feather growth: chicks consistently fledge once attaining a narrow wing length measurement irrespective of body mass (Harfenist, 1995; Deguchi et al., 2004; Takenaka et al., 2005; Sears and Hatch, 2008; Hirose et al., 2012). Experimental evidence also indicates that food-limited rhinoceros auklets have higher plasma CORT concentrations than controls (Sears and Hatch, 2008). Under the passive deposition hypothesis, differences in feather growth rates could interfere with the transfer of CORT from blood to feather tissue (Patterson et al., 2014). Thus, we predict that if feather growth is not affected by food limitation, then feather CORT will be relatively higher in nutritionally stressed chicks. We tested this prediction in the following manner: (1) we compared captive chicks reared on either control or restricted diets to test the relationships among food restriction, baseline plasma CORT and feather CORT; and (2) we measured feather CORT in free-living fledglings sampled on three colonies differing in reproductive performance to determine whether and when wild chicks experienced environmental stress.

Materials and Methods

Captive Chicks

All handling of free-living birds was conducted under the approval of the University of Alaska Fairbanks Animal Care and Use Committee protocol no. 251294-9 and sampling occurred under US Fish and Wildlife Service collection permit MB072512-1 and Alaska Department of Fish and Game permit 12-046. Importation of feathers from Japan was approved by the US Department of Agriculture (permit 115130).

We used captive-reared fledglings exposed to nutritional stress during their development (see Sears and Hatch, 2008). These birds were fed the same fish diet (the silverside, *Menidia menidia*) given *ad libitum* until 14 days post-hatch and either control (up to 75 g day^{-1}, n = 6) or restricted (up to 40 g day^{-1}, n = 6) diets thereafter. Birds were killed at 56 days post-hatch and have been stored frozen at -80 ºC since 2006 (see Bortolotti et al., 2009) for details of sampling 'old' feathers, which suggests CORT is stable in feather tissue and its concentration is unaffected by long-term storage). All chick measurements, blood collection and plasma CORT analysis were completed as part of previously reported work (Sears and Hatch, 2008). Briefly feather growth rates were calculated from measurements of the 10^{th} primary taken every 7 days from the time the feather burst through its sheath to day 42 post-hatch when feathers reached their full length of the primary at day 14 and the growth rate for the individual feather (average age at primary emergence was 11.57 days, feathers stopped growing between measurements taken at 42 and 49 days post-hatch and average growth rate was 2.2.mm day^{-1}). Blood samples (100-200 µl) of post-absorptive chicks (after overnight fasting) were collected weekly starting at age 7 days, from the alar vein within 3 min of handling to obtain a baseline measure of circulating CORT (Sears and Hatch, 2008). Plasma CORT concentrations were determined by extracting hormones with dichloromethane followed by a standard radioimmunoassay (Wingfield and Farner, 1975) with a 3% intra-assay variation and recovery values of 85-99% (Sears and Hatch, 2008).

Free-living Chicks

In 2012, free-living chicks were captured in the act of fledging (age unknown, range 42-58 days; Gaston and Dechesne, 1996) on three colonies (Teuri Island, Japan, 44º25'N, 141º18'E, n = 15 individuals; Middleton Island, Alaska, 59º26'N, 146º19'W, n = 7; St. Lazaria Island, Alaska, 56º59'N, 135º42'W, n = 13).

These three colonies encompass a broad range of environmental conditions typically experienced by breeding rhinoceros auklets. Teuri Island birds depend heavily upon lipid-rich Japanese anchovy (*Engraulis japonicas*), whose availability is affected on an inter-annual basis by a summer shift in ocean currents (Watanuki et al., 2009). Diets of breeding birds at Alaskan colonies consist of the Pacific sand

lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*) and/or greenling (*Hexagrammos decagrammus*) and change on an inter- and intra-annual basis (Thayer et al., 2008). St. Lazaria Island birds breed in a shallow continental shelf environment whereas Middleton Island birds have access to a more pelagic habitat. Typically, years that are food-rich for the Alaskan colonies are less so for the Japan colony (Thayer et al., 2008). Thus, we expected that auklets breeding at these three colonies in a given year would experience contrasting foraging conditions.

Feather Collection and Analysis

For both captive and free-living fledglings the 1st primary from the right wing was clipped at the base. After washing with distilled water and air-drying, the calamus was removed and feathers were weighed to the nearest 0.0001 g and measured to the nearest 0.5 mm. The entire feather was then divided into three 20 mm segments. Each segment was weighed to the nearest 0.0001 g and analyzed for CORT content separately. Feather segments were prepared according to Bortolotti et al., 2008 followed by a radioimmunoassay (Wingfield and Farner, 1975) using Sigma-Aldrich antibody (C 8784, St. Louis, MO, USA), intra-assay CV <2%. The Sigma-Aldrich antibody patterns of specific binding were parallel between dilution of feather CORT extract and standard CORT (Sigma-Aldrich H4001). To control for loss of CORT during the extraction process, 2000 cpm of H^3-labeled CORT (PerkinElmer NET399, Boston, MA, USA) was added to each sample and final feather CORT titers were adjusted for % recovery (mean 97%, range 80.2-100%). Assay results were normalized by converting to units of pg mm^{-1} (Bortolotti et al., 2008).

Statistical Analysis

Statistical analysis was conducted in R (R Development Team version 3.0.0). All dependent variables met assumptions of normality and homogeneity of variance. We used ANOVA to compare feather mass, length, growth rate, and age at emergence between treatments and among colonies. Sex (n = 4 males, n = 8 females) did not account for a significant amount of variation in any of the measured parameters in the experimental chicks, so it was excluded from further analyses. We used linear mixed models ('lme' function in R) to test the effect of feather segment (captive and free-living), dietary treatment (captive chicks only) and colony (free-living chicks only) on feather CORT concentrations. We included chick identity as a random factor. For all models we first tested the interactions among the fixed factors and feather mass, and removed non-significant interaction terms from final models.

Feather CORT concentrations (pg mm^{-1}) were significantly [mixed model; effect of feather segment mass (g): $F_{1,87}$=20.76, P<0.0001] and positively (parameter estimate: 392.6±260.8) correlated with the mass of feather segments in both captive and wild individuals (there was no significant

interaction between feather origin, i.e. captive versus wild, and segment mass: $F_{4,87} = 0.62$, $p = 0.65$). Thus feather mass was included as a continuous predictor in all statistical analyses and in all figures we report mass-specific feather CORT concentrations, which are the detrended values using residuals calculated from the best fit linear model for feather mass (g) and feather CORT concentrations (pg mm^{-1}).

In captive chicks, we tested the relationship between baseline plasma CORT (ng ml^{-1}) and feather CORT (pg mm^{-1}) using general linear models with baseline plasma CORT as a continuous predictor. Feather segments were matched to weekly plasma CORT samples by using the mean growth rate (2.2 mm day^{-1}) and day of emergence (11 days post-hatch) for the primaries of all captive –reared chicks. Thus, we determined that the first 20 mm of each feather (top to 20 mm) corresponded to plasma CORT on day 14, that the 21-40 mm feather segment corresponded to the average of plasma CORT concentrations measured on days 21 and 28, and that the 41 mm to base feather segment corresponded to the average of plasma CORT concentrations measured on days 35 and 42 post-hatch.

Results

Captive Chicks

We examined the 1st primary feather of chicks raised on one of two experimental diets: food restricted or control. We found that food restriction had no effect on feather mass, length, growth rate or the age at feather emergence in captive-reared chicks exposed to nutritional stress during development (Table 1.1). Because feather growth rate was unaffected by food restriction it was not included in our models.

Feathers were segmented prior to analysis to measure CORT concentration during early (feather tip to 20 mm), middle (21-50 mm) and late (41 mm to feather base) development. Feather CORT concentrations were higher in food-restricted chicks than in controls (treatment effect: $F_{1,11} = 14.69$, $p = 0.0028$; Fig. 1.1A). We observed a trend for feather CORT to increase from tip to base in both treatments (effect of segment: $F_{2,23} = 3.4$, $p = 0.051$). None of the interaction terms were significant (all $p > 0.22$).

On an individual basis, we paired feather segments (feather tip to 20 mm, 21-40 mm, and to base of feather) to baseline plasma CORT samples using growth rate measurements. We found that baseline plasma CORT (ng ml^{-1}) was not a significant predictor of CORT concentrations in feather tissues (Fig. 1.2).

Free-living Chicks

We then applied this technique to feathers collected in 2012 from fledglings on three geographically distinct colonies that differed in diet composition, oceanographic conditions, and reproductive performance: Teuri Island in Japan, and St. Lazaria Island and Middleton Island in Alaska.

Measures of reproductive success were collected on each island as part of ongoing monitoring studies. Fledging success in 2012, determined as the number of chicks fledged/number chicks hatched, was low on Teuri Island: 31% (n = 41 monitored nests). Both St. Lazaria Island and Middleton Island had reproductive success comparable to the long-term average recorded for both colonies (St. Lazaria Island: 67%, n = 148; Middleton Island: 67.3%, n = 52).

We found that free-living chicks from different colonies had similar feather mass (fixed effect ANOVA; colony effect: $F_{2,32} = 1.895$, $p = 0.167$). Feather length, measured after removal from fledglings, was not significantly different across colonies (colony effect: $F_{2,32} = 3.066$, $p = 0.061$). We found that feather CORT concentrations were affected by colony (mixed model; colony effect: $F_{2,43} = 5.94$, $p = 0.006$; Fig. 1.3) and that there were temporal differences in CORT concentration (mixed model; feather segment effect: $F_{2,65} = 16.97$, $p < 0.0001$). None of the interaction terms were significant (all $p > 0.07$).

Discussion

We used captive seabird chicks to test whether nutritional stress is reflected in an increased deposition of CORT in feather tissues. We then applied this technique to free-living chicks with unknown nutritional histories to determine whether and when individuals experienced environmental stress during their development. Feather growth did not differ significantly between treatments, ruling out effects of varying feather growth rates on feather CORT deposition. In all of our analyses we controlled for mass of the feather, thus eliminating any potential confounding effect feather mass had on CORT concentrations (Patterson et al., 2014). Feather CORT was higher in experimental chicks experiencing chronic nutritional limitation and higher in wild chicks fledged from a colony with low breeding performance.

In general, our results provide limited support for the passive deposition hypothesis (Figs. 1.1, 1.2). Sears and Hatch (2008) found a muted, but statistically significant, difference in the adrenocortical response of rhinoceros auklet chicks exposed to nutritional stress: food-limited chicks had a higher secretion of baseline CORT than controls. In this study we sampled 12 (n = 6 individuals per control and restricted diet treatments, respectively) chicks that had been killed at the conclusion of their study (other individuals were donated to a zoo for permanent housing and breeding programs). In this subset, using data previously reported by Sears and Hatch (2008), baseline plasma CORT concentrations were not different between treatments (Fig. 1.1B) and at the individual level there was no statistically significant relationship between baseline plasma and feather CORT concentrations (Fig. 1.2). The weak relationship between baseline plasma CORT and feather CORT may be due to either the relatively weak adrenocortical response of rhinoceros auklet chicks to food stress (Sears and Hatch, 2008) or to a diurnal cycle in baseline CORT secretion (Chung et al., 2011).

Furthermore, it is not unusual for the baseline plasma CORT to be highly variable, and when sample sizes are relatively small, this variability may decrease the explanatory power of independent variables. An experimental study of red-legged kittiwakes found substantial inter-individual variation in baseline plasma CORT during prolonged food restriction (Kitaysky et al., 2001); and a long-term study of free-living black-legged kittiwake (*Rissa tridactyla*) chicks found that intra-annual variability in baseline plasma CORT obscured inter-annual patterns in chick physiological status (Brewer et al., 2008). Previous studies have also found baseline plasma CORT to be a non-significant correlate with feather CORT, which was instead significantly positively correlated with stress-induced CORT (Bortolotti et al., 2008; Patterson et al., 2014). Feather CORT may, therefore, be a more robust method of detecting exposure to environmental stressors that vary in duration and intensity (see also Fairhurst et al., 2013). Like measuring the stress-induced CORT response (Kitaysky et al., 2007; Kitaysky et al., 2010), feather CORT might provide a more long-term continuous measure of an individual's exposure to elevated corticosterone, but would do so in a fraction of the handling time, under less duress to individuals, and would not have the ability to 'reset' when conditions improved.

It is also possible that baseline plasma CORT and feather CORT concentrations are composed of different components of the total CORT in circulation. The free-hormone hypothesis states that biological responses are regulated by the portion of CORT that is freely circulating in the bloodstream, and that the proportion bound to the corticosteroid-binding globulin is biologically inactive (Breuner et al., 2013). Sears and Hatch (2008) measured total CORT, which quantifies both free and bound steroids. It may be that only free CORT is deposited in feather tissues. Nevertheless, in contrast to the lack of a strong relationship with baseline plasma CORT results, and despite a reduced sample size [this study: n = 12, versus Sears and Hatch (2008): n = 26], we found a very strong signal of food restriction in feather CORT concentrations (Fig. 1.1A).

We then applied this technique to free-living chicks to determine whether feather CORT could detect exposure to environmental stress during their development in the nest. We found that feather CORT revealed whether and when chicks experienced elevated CORT levels. Feather CORT co-varied with reproductive success at the colony level, and intra-feather variation in deposition suggested that CORT was higher during some windows of development than others. For example, chicks from Teuri Island had higher concentrations of CORT in the first grown portion of their feathers and experienced overall higher stress than chicks on St. Lazaria Island (Fig. 1.3). While direct causes may vary, elevated CORT is an indicator of environmental stress (such as food shortage, inclement weather, disease, inter-sibling aggression, and predation), and indicates that perhaps poor early chick-rearing conditions contributed to the overall low fledging success on Teuri Island compared with St. Lazaria Island and Middleton Island, where reproductive success was relatively high. Rhinoceros auklets raise a single chick

in a subterranean burrow (Gaston and Dechesne, 1996) so their offspring are well protected and have little opportunity to experience environmental stress other than lack of food. It is, therefore, most likely that the early-season elevation in feather CORT concentrations we found in the free-living chicks was primarily due to food shortage.

In both captive and free-living chicks we observed temporal changes in feather CORT concentrations (Figs. 1.1, 1.3). In captive chicks there was an increasing trend in feather CORT concentrations as chicks approached fledging age. An increase in the adrenocortical function towards the end of development has been observed across avian species and is largely attributed to an upregulation of the hypothalamus-pituitary-adrenal axis in anticipation of coping with the initial stress of being independent (Corbel and Groscolas, 2008; Kozlowski et al., 2010; Wada et al., 2009; Rivers et al., 2012). While the observed increase in feather CORT concentrations over time may be due to ontogenetic processes, we cannot discount the possibility that captive chicks may have become mildly nutritionally stressed near the end of their development. In the wild, as chicks near fledging age, adult auklets have been observed to decrease their chick provisioning efforts (Bertram et al., 1991; Bertram et al., 1996), which may explain the late season increase in feather CORT concentration of free-living chicks on the Alaskan colonies (Fig. 1.3). In captive chicks, daily rations were determined based on the low and high levels of daily food intake recorded in wild chicks (Bertram et al., 1991) and did not change during chick development. Because of their static diets, all captive individuals could have experienced food limitations prior to fledging. Because of a potential interplay of pre-fledging physiology, parental decisions and changes in environmental conditions, it is difficult (and beyond the scope of our current study) to determine causal factors that explain the trends we observed in feather CORT concentrations over time. Most notable is that we were able to observe these changes in CORT secretion over time by using the continuous record of CORT deposited into growing feather tissues.

We conclude that rhinoceros auklets, seabirds that preferentially allocate limited resources to wing and feather growth and retain an adrenocortical response to food limitation during development, deposit higher concentrations of CORT in growing feather tissue in response to nutritional stress. We also found that feather CORT can detect food limitation in rhinoceros auklet chicks when baseline plasma CORT does not. Our results demonstrate that feather CORT can be used to make spatial and temporal comparisons of environmental conditions and reveal specific periods, and durations of stress experienced by seabird chicks during their development. This relatively non-invasive technique, when applied appropriately, could provide important physiological information to evolutionary and ecological studies of free-living seabirds.

Acknowledgements

We would like to thank R.C. Young and Z.M. Benowitz-Fredericks and an anonymous reviewer for their comments and edits, which greatly improved this manuscript. This work was made possible by the North Pacific Research Board (publication 497), University of Alaska Fairbanks' Institute of Arctic Biology, and Friends of Alaska's National Wildlife Refuges. We would like to thank the Alaska Maritime National Wildlife Refuge for field support.

References

Astheimer, L. B., Buttemer, W. A. and Wingfield, J. C. (1992). Interactions of corticosterone with feeding, activity and metabolism in Passerine birds. *Ornis Scandinavica* **23**, 355-365.

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W. and Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behav. Ecol.* **23**, 960-969.

Bertram, D. F., Kaiser, G. W. and Ydenberg, R. C. (1991). Patterns in the provisioning and growth of nestling rhinoceros auklets. *Auk* **108**, 842-852.

Bertram, D. F., Welham, C. V. J. and Ydenberg, R. C. (1996). Flexible effort in breeding seabirds: adjustment of provisioning according to nestling age and mass. *Can. J. Zool.* **74**, 1876-1881.

Blas, J., Bortolotti, G. R., Tella, J. L., Baos, R. and Marchant, T. A. (2007). Stress response during development predicts fitness in a wild, long lived vertebrate. *Proc. Natl. Acad. Sci. USA* **104**, 8880-8884.

Bortolotti, G. R., Marchant, T. A., Blas, J. and German, T. (2008). Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Funct. Ecol.* **22**, 494-500.

Bortolotti, G. R., Marchant, T., Blas, J. and Cabezas, S. (2009). Tracking stress: localization, deposition and stability of corticosterone in feathers. *J. Exp. Biol.* **212**, 1477-1482.

Breuner, C. W., Delehanty, B. and Boonstra, R. (2013). Evaluating stress in natural populations of vertebrates: total CORT is not good enough. *Funct. Ecol.* **27**, 24-36.

Brewer, J. H., O'Reilly, K. M., Dean Kildaw, S. and Loren Buck, C. (2008). Inter-annual variation in the adrenal responsiveness of black-legged kittiwake chicks (*Rissa tridactyla*). *Gen. Comp. Endocrinol.* **156**, 361-368.

Buck, C. L., O'Reilly, K. M. and Kildaw, S. D. (2007). Inter-annual variability of blacklegged kittiwake productivity is reflected in baseline plasma corticosterone. *Gen. Comp. Endocrinol.* **150**, 430-436.

Chung, S., Son, G. H. and Kim, K. (2011). Adrenal peripheral oscillator in generating the circadian glucocorticoid rhythm. *Ann. N. Y. Acad. Sci.* **1220**, 71-81.

Corbel, H. and Groscolas, R. (2008). A role for corticosterone and food restriction in the fledging of nestling white storks. *Horm. Behav.* **53**, 557-566.

Deguchi, T., Takahashi, A. and Watanuki, Y. (2004). Proximate factors determining age and mass at fledging in rhinoceros auklets (*Cerorhinca monocerata*): intra- and inter-year variations. *Auk* **121**, 452-462.

Dehnhard, N., Poisbleau, M., Demongin, L., Chastel, O., van Noordwijk, H. J. and Quillfeldt, P. (2011). Leucocyte profiles and corticosterone in chicks of southern rockhopper penguins. *J. Comp. Physiol. B* **181**, 83-90.

Doody, L. M., Wilhelm, S. I., McKay, D. W., Walsh, C. J. and Storey, A. E. (2008). The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. *Horm. Behav.* **53**, 140-148.

Dorresteijn, I., Kitaysky, A. S., Barger, C., Benowitz-Fredericks, Z. M., Byrd, G. V., Schultz, M. and Young, R. (2012). Climate affects food availability to planktivorous least auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea. *Mar. Ecol. Prog. Ser.* **454**, 207-220.

Fairhurst, G. D., Frey, M. D., Reichert, J. F., Szelest, I., Kelly, D. M. and Bortolotti, G. R. (2011). Does environmental enrichment reduce stress? An integrated measure of corticosterone from feathers provides a novel perspective. *PLoS ONE* **6**, e17663.

Fairhurst, G. D., Navarro, J., González-Solís, J., Marchant, T. A. and Bortolotti, G. R. (2012a). Feather corticosterone of a nestling seabird reveals consequences of sex-specific parental investment. *Proc. R. Soc. B* **279**, 177-184.

Fairhurst, G. D., Treen, G. D., Clark, R. G. and Bortolotti, G. R. (2012b). Nestling corticosterone response to microclimate in an altricial bird. *Can. J. Zool.* **90,** 1422-1430.

Fairhurst, G. D., Marchant, T. A., Soos, C., Machin, K. L. and Clark, R. G. (2013). Experimental relationships between levels of corticosterone in plasma and feathers in a free-living bird. *J Exp. Biol.* **216**, 4071-4081.

Gaston, A. J. and Dechesne, S. B. (1996). Rhinoceros Auklet (*Cerorhinca monocerata*). In *The Birds of North America Online* (ed. A. Poole). Ithaca, NY: Cornell Laboratory of Ornithology. Available at: http://bna.birds.cornell.edu/bna/species/212

Goutte, A., Angelier, F., Welcker, J., Moe, B., Clément-Chastel, C., Gabrielsen, G. W., Bech, C. and Chastel, O. (2010). Long-term survival effect of corticosterone manipulation in Black-legged kittiwakes. *Gen. Comp. Endocrinol.* **167**, 246-251.

Harding, A. M. A., Kitaysky, A. S., Hall, M. E., Welcker, J., Karnovsky, N. J., Talbot, S. L., Hamer, K. C. and Grémillet, D. (2009). Flexibility in the parental effort of an Arctic-breeding seabird. *Funct. Ecol.* **23**, 348-358.

Harding, A. M. A., Welcker, J., Steen, H., Hamer, K. C., Kitaysky, A. S., Fort, J., Talbot, S. L., Cornick, L. A., Karnovsky, N. J., Gabrielsen, G. W. et al. (2011). Adverse foraging conditions may impact body mass and survival of a high Arctic seabird. *Oecologia* **167**, 49-59.

Harfenist, A. (1995). Effects of growth-rate variation on fledging of rhinoceros auklets (*Cerorhinca monocerata*). *Auk* **112**, 60-66.

Herring, G., Cook, M. I., Gawlik, D. E. and Call, E. M. (2011). Food availability is expressed through physiological stress indicators in nestling white ibis: a food supplementation experiment. *Funct. Ecol.* **25**, 682-690.

Hirose, F., Kazama, K., Ito, M. and Watanuki, Y. (2012). Accelerated growth rates in late-hatched rhinoceros auklet *Cerorhinca monocerata* chicks depend on food conditions and growth stage: an experimental approach. *Ibis* **154**, 296-306.

Honarmand, M., Goymann, W. and Naguib, M. (2010). Stressful dieting: nutritional conditions but not compensatory growth elevate corticosterone levels in zebra finch nestlings and fledglings. *PLoS ONE* **5**, e12930.

Jacobs, S. R., Elliott, K. H. and Gaston, A. J. (2013). Parents are a drag: long-lived birds share the cost of increased foraging effort with their offspring, but males pass on more of the costs than females. *PLoS ONE* **8**, e54594.

Kitaysky, A. S., Piatt, J. F., Wingfield, J. C. and Romano, M. (1999). The adrenocortical stress-response of black-legged kittwake chicks in relation to dietary restrictions. *J. Comp. Physiol. B* **169**, 303-310.

Kitaysky, A. S., Kitaiskaia, E. V., Wingfield, J. C. and Piatt, J. F. (2001). Dietary restriction causes chronic elevation of corticosterone and enhances stress response in red-legged kittiwake chicks. *J. Comp. Physiol. B* **171**, 701-709.

Kitaysky, A. S., Kitaiskaia, E. V., Piatt, J. F. and Wingfield, J. C. (2003). Benefits and costs of increased levels of corticosterone in seabird chicks. *Horm. Behav.* **43**, 140-149.

Kitaysky, A. S., Piatt, J. F. and Wingfield, J. C. (2007). Stress hormones link food availability and population processes in seabirds. *Mar. Ecol. Prog. Ser.* **352**, 245-258.

Kitaysky, A. S., Piatt, J. F., Hatch, S. A., Kitaiskaia, E. V., Benowitz-Fredericks, Z. M., Shultz, M. T. and Wingfield, J. C. (2010). Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Funct. Ecol.* **24**, 625-637.

Kouwenberg, A., Hipfner, J. M., McKay, D. W. and Storey, A. E. (2013). Corticosterone and stable isotope in feathers predict egg size in Atlantic puffins *Fratercula arctica*. *Ibis* **155**, 413-418.

Kozlowski, C. P., Mauck, R. A., O'Reilly, K. M., Philipsborn, J. and Ricklefs, R. E. (2010). Changes in plasma hormone levels correlate with fledging in nestling Leach's storm-petrels. *Gen. Comp. Endocrinol.* **169**, 91-97.

Lattin, C. R., Reed, D., DesRochers, D. W. and Romero, L. M. (2011). Elevated corticosterone in feathers correlates with corticosterone-induced decreased feather quality: a validation study. *J. Avian Biol.* **42**, 247-252.

Müller, C., Jenni-Eiermann, S. and Jenni, L. (2009). Effects of a short period of elevated circulating corticosterone on postnatal growth in free-living Eurasian kestrels *Falco tinnunculus*. *J. Exp. Biol.* **212**, 1405-1412.

Patterson, A. G. L., Kitaysky, A. S., Lyons, D. E. and Roby, D. D. (2014). Nutritional stress affects corticosterone deposition in feathers of Caspian tern chicks. *J. Avian Biol.* **46** , 18-24.

Pravosudov, V. V. and Kitaysky, A. S. (2006). Effects of nutritional restrictions during post-hatching development on adrenocortical function in western scrub-jays (*Aphelocoma californica*). *Gen. Comp. Endocrinol.* **145**, 25-31.

Rivers, J. W., Liebl, A. L., Owen, J. C., Martin, L. B. and Betts, M. G. (2012). Baseline corticosterone is positively related to juvenile survival in a migrant passerine bird. *Funct. Ecol.* **26**, 1127-1134.

Satterthwaite, W. H., Kitaysky, A. S., Hatch, S. A., Piatt, J. F. and Mangel, M. (2010). Unifying quantitative life-history theory and field endocrinology to assess prudent parenthood in a long-lived seabird. *Evol. Ecol. Res.* **12**, 779-792.

Satterthwaite, W. H., Kitaysky, A. S. and Mangel, M. (2012). Linking climate variability, productivity and stress to demography in a long-lived seabird. *Mar. Ecol. Prog. Ser.* **454**, 221-235.

Schoech, S. J., Rensel, M. A. and Heiss, R. S. (2011). Short- and long-term effects of developmental corticosterone exposure on avian physiology, behavioral phenotype, cognition and fitness: a review. *Curr. Zool.* **57**, 514-530.

Sears, J. and Hatch, S. A. (2008). Rhinoceros auklet developmental responses to food limitation: an experimental study. *Condor* **110**, 709-717.

Spencer, K. A., Evans, N. P. and Monaghan, P. (2009). Postnatal stress in birds: a novel model of glucocorticoid programming of the hypothalamic-pituitary-adrenal axis. *Endocrinology* **150**, 1931-1934.

Takenaka, M., Niizuma, Y. and Watanuki, Y. (2005). Resource allocation in fledglings of the rhinoceros auklet under different feeding conditions: an experiment manipulating meal size and frequency. *Can. J. Zool.* **83**, 1476-1485.

Thayer, J. A., Bertram, D. F., Hatch, S. A., Hipfner, M. J., Slater, L., Sydeman, W. J. and Watanuki, Y. (2008). Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. *Can. J. Fish. Aquat. Sci.* **65**, 1610-1622.

Wada, H., Salvante, K. G., Wagner, E., Williams, T. D. and Breuner, C. W. (2009). Ontogeny and individual variation in the adrenocortical response of zebra finch (*Taeniopygia guttata*) nestlings. *Physiol. Biochem. Zool.* **82**, 325-331.

Watanuki, Y., Ito, M., Deguchi, T. and Minobe, S. (2009). Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. *Mar. Ecol. Prog. Ser.* **393**, 259-271.

Wingfield, J. C. and Farner, D. S. (1975). The determination of five steroids in avian plasma by radioimmunoassay and competitive protein-binding. *Steroids* **26**, 311-327.

Figures

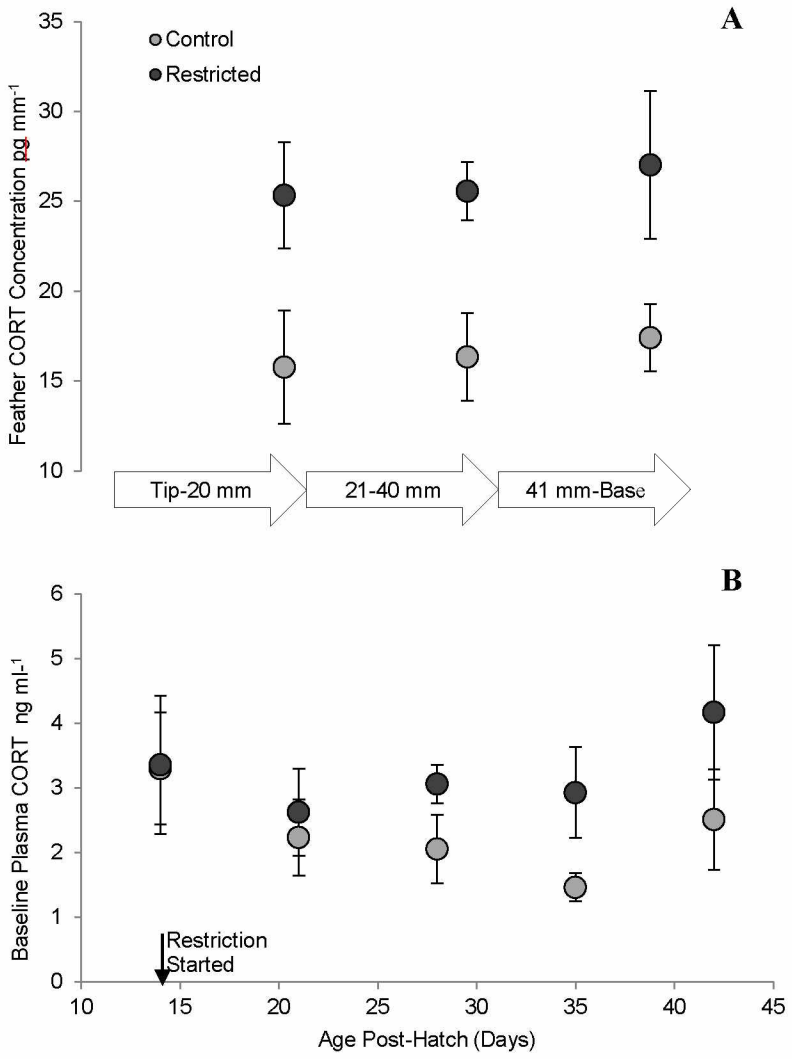

Figure 1.1 Food limitation results in higher feather corticosterone (CORT) concentrations. (A) Mean (± s.e.m.) feather CORT concentration (controlled for the mass of the feather segment) in the first primary feather (grown between ~11 and 42 days post-hatch) of control (n = 6) and restricted (n = 6) rhinoceros auklet chicks, shown by feather segment (growth period indicated by arrows). (B) Mean (± s.e.m.) baseline plasma CORT concentrations (measured weekly between 14 and 42 days post-hatch) of control (n = 6) and restricted (n = 6) rhinoceros auklet chicks were not significantly different (mixed model; effect of treatment: $F_{1,10} = 2.17$, $p = 0.17$, effect of age: $F_{1,46} = 0.009$, $p = 0.92$; interaction between treatment and age: $F_{1,46} = 2.04$, $p = 0.16$). Plasma CORT values are for 12 of the 26 chicks included in results reported previously (see Sears and Hatch, 2008).

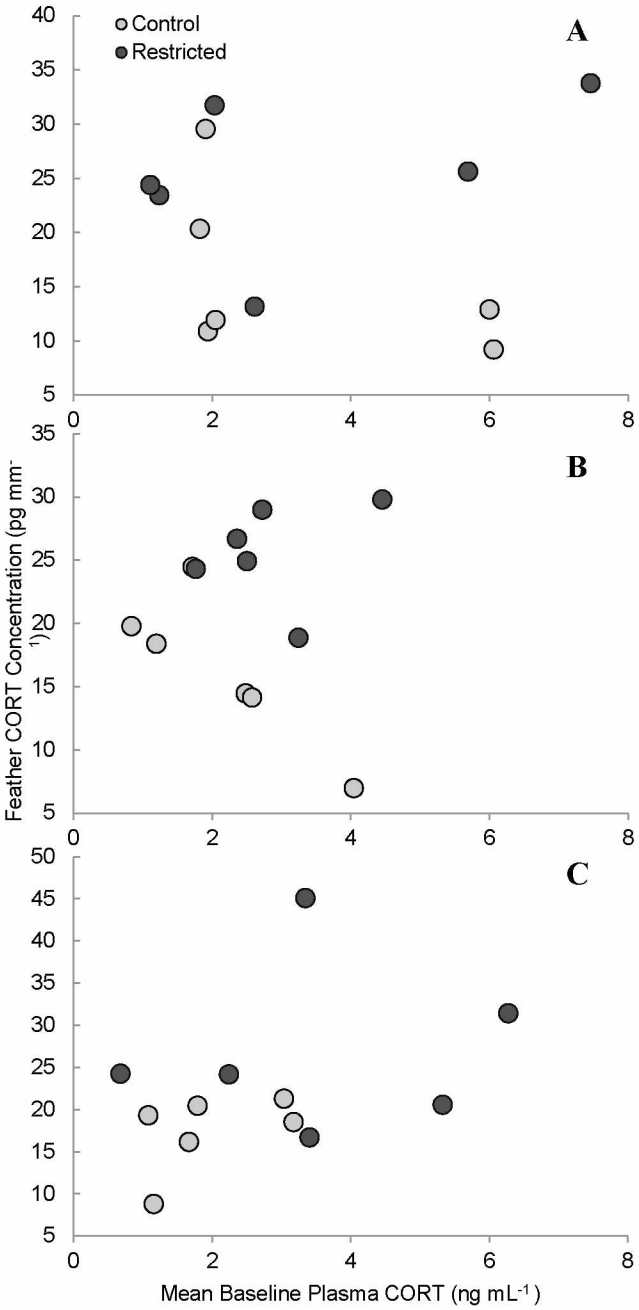

Figure 1.2 Baseline plasma CORT is not significantly correlated with feather CORT concentrations. Feather CORT concentrations (controlled for the mass of the feather segment) are reported for (A) the first segment (tip to 20 mm) paired with baseline plasma CORT collected on day 14 ($F_{1,10} = 0.002$, $p = 0.96$, $R^2 < 0.001$), (B) the second segment (21–40 mm) paired with the mean concentration of baseline plasma CORT collected on days 21 and 28 ($F_{1,10} = 0.04$, $p = 0.84$, $R^2 = 0.004$), and (C) the third segment (41 mm to base) paired with the mean concentration of baseline plasma CORT collected on days 35 and 42 ($F_{1,10} = 1.77$, $p = 0.21$, $R^2 = 0.15$). Captive rhinoceros auklet chicks are coded by treatment for illustrative purposes only: control n = 6, restricted n = 6.

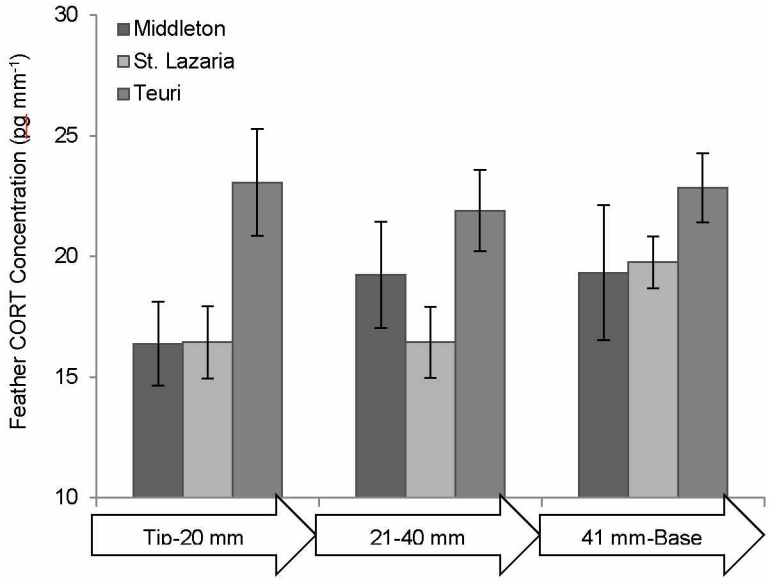

Figure 1.3 Feather CORT concentrations of free-living rhinoceros auklet chicks. Reported are mean (± s.e.m.) feather CORT concentrations (controlled for the mass of the feather segment) in three different segments (from tip, grown first, to the base, grown last as indicated by the arrows) of the first primary feather tissues.

Table

Table 1.1 Parameters of feather growth and development were not significantly different between rhinoceros auklet chicks raised on control and restricted diets. Means ± s.e.m., and corresponding statistical parameters.

Feather Parameters	Control	Restricted	ANOVA	
			$F_{1,11}$	p-value
Mass (g)	0.029 ± 0.002	0.03 ± 0.001	0	0.99
Length (mm)	59.69 ± 1.27	59.21 ± 1.15	0.167	0.69
Growth Rate (mm/day)	2.22 ± 0.02	2.18 ± 0.04	1.163	0.3
Age at Primary Emergence (days)	11.61 ± 0.24	11.56 ± 0.26	0.03	0.87

Chapter 2 Feather Corticosterone Reveals Stress Associated with Dietary Changes in a Breeding Seabird.[2]

Abstract

Changes in climate and anthropogenic pressures might affect the composition and abundance of forage fish in the world's oceans. The junk-food hypothesis posits that dietary shifts that affect the quality (e.g., energy content) of food available to marine predators may impact their physiological state and consequently affect their fitness. Previously we experimentally validated that deposition of the adrenocortical hormone, corticosterone, in feathers is a sensitive measure of nutritional stress in seabirds. Here we use this method to examine how changes in diet composition and prey quality affect the nutritional status of free-living rhinoceros auklets (*Cerorhinca monocerata*). Our study sites included: Teuri Is. Japan, Middleton Is. central Gulf of Alaska, and St. Lazaria Is. Southeast Alaska. In 2012 and 2013 we collected "bill loads" delivered by parents to feed their chicks (n = 758) to document dietary changes. We deployed time-depth-temperature recorders on breeding adults (n = 47) to evaluate whether changes in prey coincided with changes in foraging behavior. We measured concentrations of corticosterone in fledgling (n = 71) and adult breeders' (n = 82) feathers to determine how birds were affected by foraging conditions. We found that seasonal changes in diet composition occurred on each colony, adults dove deeper and engaged in longer foraging bouts when capturing larger prey, and that chicks had higher concentrations of corticosterone in their feathers when adults brought back smaller and/or lower energy prey. Corticosterone levels in feathers of fledglings (grown during the breeding season) and those in feathers of adult breeders (grown during the post-breeding season) were positively correlated, indicating possible carry-over effects. These results suggest that seabirds might experience increased levels of nutritional stress associated with moderate dietary changes; and that physiological responses to changes in prey composition should be considered when evaluating the effect of prey quality on marine predators.

[2] Will, Alexis; Watanuki,Yutaka; Kikuchi, Dale M;. Sato, Nobuhiko; Ito, Motohiro; Callahan, Matt; Wynne-Edwards, Katherine; Hatch, Scott; Elliott, Kyle; Slater, Leslie; Takahashi, Akinori; Kitaysky, Alexander. Ecology and Evolution. September 2015. doi: 10.1002/ece3.1694.

Introduction

Ecological changes such as increased competition (e.g., Svanbäck and Bolnick, 2007), disease (e.g., Moleón et al., 2009), or fluctuations in the availability and abundance of food (e.g., Zhou et al., 2015, Jackson and Rundle, 2008) can result in short-term changes in the composition and quality (e.g., energy content) of an animal's diet. According to the junk-food hypothesis, changes in the quality of prey can affect a marine animal's ability to survive and reproduce (Alverson, 1992). Climate change and anthropogenic pressures might induce shortages in the availability of energy-rich prey to marine predators, such as seabirds (Kitaysky et al., 2006, Essingtona et al., 2015); yet studies of how prey quality affects reproductive performance in seabirds provide mixed support for the junk-food hypothesis. Some studies find no evidence that changes in prey quality affect reproductive output (Jodice et al., 2006, Kadin et al., 2012, Hjernquist and Hjernquist, 2010). Others clearly demonstrate that low-quality prey, such as fisheries offal (Grémillet et al., 2008), or changes in the energy content, availability, or abundance of a preferred energy-rich prey species (Wanless et al., 2007, Dorresteijn et al., 2012, Barrett et al., 2015), negatively impact reproductive performance and adult nutritional status (Dorresteijn et al., 2012, Barrett et al., 2015).

The impact of prey quality (i.e., total caloric content which is often driven by lipid richness) and quantity may be best examined on a continuum, with switches between prey of equal quality on one end and changes between high and low quality prey at the other. With this approach, we expect that a switch from high- to low-quality prey would only impact reproductive performance and/or survival in cases where prey quality changed substantially and could not be counteracted by increasing the quantity of the low-quality food. If switches occur among prey of relatively equal energy value, overall reproductive performance may not vary, but the physiology and behavior of individuals may be affected.

Many seabird species (e.g., see Rector et al., 2012, Benowitz-Fredericks et al., 2008, Kitaysky et al., 1999) respond to nutritional stress with increased levels of the avian stress hormone, corticosterone (CORT). Researchers use concentrations of CORT as a relative measure to infer the nutritional stress that birds incur. Nutritional stress occurs when individuals experience a negative balance between their energy needs and the energy that is available (Kitaysky et al., 2001b). The increased secretion of CORT in response to a decrease in energy intake enables an individual to survive the event (Kitaysky et al., 2003, Kitaysky et al., 2001a), but stress incurred during the event can take a toll, impacting their ability to survive and reproduce in the future (Kitaysky et al., 2010). To test how changes in prey composition and quality affect seabirds, we examined the chick diets, adult behavior, and the stress status of chick and adult rhinoceros auklets (*Cerorhinca monocerata*, hereafter RHAU, Fig. 2.1), a coastal, pursuit-diving piscivore that breeds in the North Pacific.

First, we examined how chick diets changed over the course of the breeding season. Then we focused our investigation on the relationship between diet and adult foraging behavior, which may mediate the impact of diet changes on both adults and chicks. In cases of mild or temporary food shortages, breeding seabirds may adjust their foraging behavior (e.g. Burke and Montevecchi, 2009, Harding et al., 2009, Harding et al., 2013) by increasing dive frequency (Hedd et al., 2009, Ronconi and Burger, 2008), the number of foraging bouts, and/or the time spent underwater in pursuit of prey (Karnovsky et al., 2011).

Finally we examined the concurrent physiological status of chicks and the post-reproductive status of adults. We measured CORT in feather tissues to assess whether changes in diet composition affected physiology. Previously we have shown that experimentally induced nutritional stress is associated with higher concentrations of CORT in RHAU fledglings' feathers (Will et al., 2014). This endocrine technique allows for a one-time handling of fledglings to obtain an integrated measure of stress physiology (Bortolotti et al., 2008) during the growth of the sampled feather (up to 48 days, Gaston and Dechesne, 1996). We predicted that changes from high to low quality prey would affect parental foraging behavior and result in elevated CORT concentrations in fledgling and adult feathers.

Methods

Study Sites

We chose three colonies which differ dramatically in their oceanography and prey dynamics. Fieldwork occurred in 2012, 2013, and 2014 (a follow-up year to collect adult feathers) on: St. Lazaria Island (56°59'N 135°42'W), 22 km west of Sitka, Alaska at the entrance to Sitka Sound in the Eastern Gulf of Alaska (Fig. 2.1) and home to ~2,000 pairs of breeding RHAU that prey heavily upon capelin (*Mallotus villosus*) and Pacific sand lance (*Ammodytes hexapterus*) (Hovis and Slater, 2012, Slater and Byrd, 2009). Middleton Island (59°26'N 146°19'W), in the Northern Gulf of Alaska (Fig. 2.1), has 7,500 to 10,000 breeding pairs (S. Hatch pers. comm.) that feed predominantly on capelin (Hatch, 2013). Teuri Island (44°25'N: 141°18'E), in Northern Japan (Fig. 2.1), where the world's largest population of RHAUs (~300,000 breeding pairs) provision their young primarily with Japanese anchovy (*Engraulis japonicus*) (Watanuki et al., 2009).

Study Species

RHAUs are nocturnal, burrow-nesting seabirds, with bi-parental care of a single chick. Chicks receive at most two meals per night (one per parent) delivered as a "bill load", a collection of whole fish which adults carry crosswise in their bill (Fig. 2.1, Gaston and Dechesne, 1996). Across much of their range RHAU reproductive success correlates positively with the presence of a particular prey species in

their chicks' diet (Hedd et al., 2006, Watanuki and Ito, 2012). Experimental work indicates that RHAU chicks preferentially allocate limited resources to the growth and development of organs and skeletal structures needed for fledging (Takenaka et al., 2005, Hirose et al., 2012), and retain a typical physiological response (increased CORT) to reduced caloric intake (Sears and Hatch, 2008, Will et al., 2014). Chick diet composition closely resembles parental diet during the chick-rearing period (Ito et al., 2009, Hipfner et al., 2013).

Chick Diet

We collected bill loads from parents throughout the chick-rearing period (late June-August St. Lazaria and Middleton, and late May-July Teuri) to assess changes in diet composition. While bill loads were collected during capture and recapture of adults outfitted with TDRs, the greater portion of samples were collected from birds not participating in that aspect of the study. These birds were intercepted on the ground as they returned to the colony at dusk. Fish were identified to species or, for greenling (*Hexigrammidae spp.*) to genus, individually weighed, measured and, on St. Lazaria, frozen in the field for post-season energy content analysis. For both 2012 and 2013 we sampled eight capelin, greenling, Pacific herring (*Clupea pallasii*), Pacific sand lance, and salmon species (*Oncorhynchus spp.*), for a total of 16 fish per species, except herring which was nearly absent from 2012 bill loads. Fish sampled were of average length and collected throughout the study period. Individual fish were homogenized using a mortar and pestle and dried with a Leco Thermogravimetric Analyzer (St. Joseph, Michigan, USA), which also measured moisture content. Dried samples were crushed into powder and pressed into 150-200 mg pellets for bomb calorimetry. Energy density (kJ g-1 dry) was determined using a Parr 6725 semi micro calorimeter (Moline, Illinois, USA); see Siddon et al. (2013) for full method details. Energy content for fish from other islands was derived from previously published values (Takahashi et al., 2001, Van Pelt et al., 1997). Bill load energy content was determined by multiplying the energy content (wet mass: kJ g-1) for each fish species by the field-recorded mass of the individual fish and the products summed for all fish in each complete bill load.

Adult Foraging Behavior

On St. Lazaria breeding adult rhinoceros auklets were captured at night while entering their burrows. G5 Cefas (Cefas Technologies Ltd, Lowestoft, Suffolk, UK) time-depth-temperature recorders (TDR) were mounted on a size 5 plastic tarsal band (Pro Touch Engraving, Saskatoon, SK, Canada) using 5-minute epoxy and two zip-ties. The entire assembly weighed ~ 4 g; < 1% of the average St. Lazaria RHAU's body mass. Loggers were pre-programmed to collect data for two to five days and were deployed throughout the chick-rearing period beginning in early July and continuing through mid-August.

Recapture effort began the day before tags finished logging and, in some cases, continued until the end of the season. We recovered 50% and 83% of tags in 2012 and 2013 respectively.

On Teuri adults were captured at night in their burrows. Birds were outfitted with accelerometers (ORI-D3GT: ϕ12×45 mm, 9 g, Little Leonardo Corp., Tokyo, Japan) that also recorded temperature and diving depth. Loggers recorded data for one or two days, and were deployed during a one week period mid-way through the breeding season (for details see Kikuchi et al., 2015).

No dive data are available for Middleton. TDRs (LAT290, Lotek Marine Technology, St. John's, Newfoundland, Canada) were deployed but the tag settings made the data incomparable to data from St. Lazaria and Teuri.

Adults were sexed genetically using erythrocyte extracted DNA and amplification of the CHD1 gene (Griffiths et al., 1998), and morphologically sexed using a discriminant equation (96% probability of correct differentiation) based on bill measurements (Niizuma et al., 1999).

Chick and Adult Nutritional Stress

We captured chicks in the act of fledging (parents and age unknown, range 42-58 days old; Gaston and Dechesne, 1996) and sampled their first primary (P1, clipped at the base), grown from day 10 – 49 post-hatch (Will et al., 2014). Feathers were prepared according to Will et al. (2014) and Bortolotti et al. (2008). Briefly, the entire feather was divided into three 20 mm segments to be analyzed for CORT (hereafter fCORT) separately for measures of early, middle, and late feather growth stress status. Each segment was minced, and then extracted in 7 ml methanol (HPLC-grade, Fisher Scientific, Waltham, Massachusetts, USA). Feather segments were analyzed in a radioimmunoassay (Wingfield and Farner, 1975) using a Sigma-Aldrich antibody (C 8784, Saint Louis, Missouri, USA), intra-assay CV < 1% and inter-assay (3 assays) CV 1.5%. To control for loss of CORT during the extraction process 2,000 cpm of H3-labeled CORT (PerkinElmer NET399, Boston, Massachusetts, USA) was added to each sample and final fCORT titers were adjusted for % recovery (mean = 89%). Assay results were normalized by converting to units of pg mm-1 (Bortolotti et al., 2008). Results from 2012 appeared previously in Will et al. (2014) as part of a validation study.

RHAU undergo a sudden post-reproductive molt of their primary feathers (Gaston and Dechesne, 1996) thus in any given breeding season, it is possible that adult fCORT reflects physiological status at the end of the previous breeding season. We measured carry-over effects of the breeding to post-reproductive season by recapturing breeding individuals the subsequent year (capture and handling during the previous year had no effect on fCORT concentrations, A. Will unpubl. data). Upon recapture we sampled the first primary (all colonies, all years except Teuri, 2013 when the 10th primary was sampled, fCORT concentrations were within the ranges measured in P1). On St. Lazaria feathers were collected

from TDR birds caught in 2013 and again in 2014, however on Teuri and Middleton samples were collected from untagged breeding adults. Feather growth rate for adult RHAU is not well known, but assuming a similarity with their close relative, the tufted puffin, *Fratercula cirrhata* (Thompson and Kitaysky, 2004), we estimate that the adult feather segments we analyzed were grown during ~10 days at the start of the post-reproductive molt. Feathers were prepared and analyzed following the same protocol as for chicks with the following exceptions: only 25 mm of the tip was sampled for analysis, washed with deionized water and isopropanol (HPLC-grade, Sigma-Aldrich, St. Louis, Missouri, USA) to remove dirt and oils, and extracted intact. Intra-assay CV <1%, inter-assay (3 assays) CV 5.9% and final fCORT titers were adjusted for % recovery (mean = 95.8%).

The Sigma antibody used in our assay has a high affinity for corticosterone but also demonstrates some cross-reactivity with other steroids; therefore, we also verified the presence of the corticosterone molecule in both chick and adult primary feather tissues using high-performance liquid chromatography tandem mass-spectrometry (Appendix 1, Koren et al., 2012).

Statistical Analysis

We divided the breeding season into "Early" and "Late" periods to evaluate intra-annual changes in chick diet and adult foraging behavior. Due to the timing of when samples and adult behaviors were recorded we could not further divide these variables into three intervals to match the fledgling feather segments because some intervals would have no data points. These periods were determined by using the average length of primary feathers collected from fledglings for a given island to back-calculate from the average fledgling capture date. We assumed primaries grew at 2.2 mm/day (Will et al., 2014), then divided the total days of the feather growth period in half. We subtracted this number from the average fledgling capture date to arrive at the boundary of "Early" and "Late" chick-rearing.

Adult Foraging Behavior— TDR data was first processed in IGOR Pro (WaveMetrics 2008) following Ito et al. (2010) to summarize the duration (sec) and depth (m) of each recorded dive. We calculated a bout-ending criterion following Sibly et al. (1990) for each colony and each year. Using this value we assigned dives to foraging bouts and calculated the number of dives per bout, how long (sec) the bout lasted (bout duration), and the average depth (m) of dives in a bout (average bout depth) for each bird. We also calculated the number of bouts that occurred each day and the total time (sec) a bird spent underwater in a day. All dive parameters, except for time underwater, were severely right-skewed; therefore, we used general linear mixed models (*lme4* package in R) with bird as a random factor and either a Poisson or, to account for overdispersion in the data, a negative binomial distribution. All models were evaluated with a goodness of fit test and returned a $\chi^2 = 1$. Dive depth was converted to whole numbers and time underwater was square-root transformed to satisfy assumptions of count-values

(Poisson) and normal distribution (linear model) respectively. Because we were primarily interested in overall differences in diving behavior between years we excluded sex from our final models due to small sample sizes in both years on Teuri. However, before exclusion we ran the models with sex to verify that it did not alter the results. Finally we were unable to run a model comparing diving behavior to diets because the number of TDR birds with associated diets was too low and restricted to St. Lazaria.

Chick and Adult Nutritional Stress Status—fCORT concentrations (pg mm-1) were log-transformed to meet assumptions of normality and were significantly (mixed model with Fledgling as a random factor; effect of feather segment mass, g: $F_{1,143} = 76.45$, $p < 0.0001$) and positively (parameter estimate: 739.93 ± 84.62) correlated with feather segment mass. Therefore, we detrended fCORT values by using residuals calculated from the best fit linear model of log-transformed feather mass ($\log_{10}$(g)) and log-transformed fCORT concentrations ($\log_{10}$(pg mm-1)) for chicks and adults separately. We use these detrended values in all figures and statistical analyses. Previously we showed that sex does not affect fledgling's fCORT (Will et al., 2014), nor did we find a significant difference between fCORT concentrations in adult male and female feather tissues ($t_{33} = 0.18$, $p = 0.43$); so we did not include sex in our analysis. All analyses were completed in R (version 3.1.2). For each analysis we tested and report the full model.

Results

Chick Diet

Bill-load energy content attributed to a preferred prey: capelin on St. Lazaria and Middleton, and Japanese anchovy on Teuri (Table 2.1), changed on all three islands in both years. On Middleton and St. Lazaria, when birds did not return with capelin they delivered species whose energy content was similar, such as herring and sand lance. Whereas when Japanese anchovy were not available on Teuri, adults made up the difference with lower quality prey (Table 2.1 and 2.2). Similarly on Middleton and St. Lazaria, pink salmon and greenling, respectively, constituted >10% of the diet at times and are not has high in caloric value as the other three primary prey species (capelin, sand lance, and herring) at those locations.

Adult Behavior

Adult diving behavior varied significantly both between colonies and between years. Bout duration and bout depth were greater for Teuri birds than for those on St. Lazaria, but dives per bout and bouts per day were fewer (see Table 2.3). Birds on both colonies had more foraging bouts per day and spent more time underwater in 2013 than in 2012.

On St. Lazaria in 2012, tagged adult RHAU more often skipped returning to the colony at least one night during tag deployment compared to 2013 (Fisher's exact test $p = 0.03$; 2012 proportion that skipped = 0.44, n = 9; 2013 proportion that skipped = 0.06, n = 18).

Chick and Adult Nutritional Stress Status

In general RHAU chicks experienced higher nutritional stress in 2012 than in 2013 on all colonies (mixed model fixed factor, Year: parameter estimate = -0.46, $F_{1,66} = 34.067$, $p = < 0.0001$, Fig. 2.2). Chicks reared on different colonies had different fCORT concentrations (fixed factor, Colony: $F_{2,66} = 10.282$, $p = 0.0001$). Nutritional stress changed significantly over the course of the chick-rearing period in both years (fixed factor, Feather Segment: Fig. 2.2, $F_{2,138} = 16.43$, $p = 0.0001$). However, fCORT concentration within a season decreased in 2012 and increased in 2013 (interaction term, Year*Feather Segment: $F_{1,138} = 89.96$, $p = < 0.0001$). While this pattern occurred on all three colonies, inter-colony differences in fCORT were still detectable within each feather segment (interaction term Colony*Feather Segment: $F_{2,138} = 3.512$, $p = 0.032$). All other variables did not explain a significant proportion of the variability in the fCORT concentrations (interaction terms Colony*Year: $F_{2,66} = 0.89$, $p = 0.42$, Colony*Year*Feather Segment: $F_{2,138} = 0.05$, $p = 0.95$).

Bill-load energy content did not differ between years (ANOVA, Year: $F_{1,10} = 0.21$, $p = 0.65$) but was different between colonies (ANOVA, Colony: $F_{2,10} = 3.99$, $p = 0.05$). The seasonal pattern of bill-load energy content among colonies tended to differ between years (ANOVA, Year*Colony: $F_{2,10} = 3.66$, $p = 0.06$) and within years (ANOVA, Year*Segment: $F_{1,10} = 4.55$, $p = 0.06$). Bill-load mass was correlated to bill-load energy content (simple linear regression: adjusted-$R^2 = 0.8$, $p = < 0.001$). However, fCORT by feather growth period (early, middle, late) corresponded more to changes in bill-load energy content (mixed model, feather segment as a random factor: $F_{1,11} = 7.24$, $p = 0.02$, Fig. 2.3), than to changes in bill-load mass (mixed model: $F_{1,11} = 3.82$, $p = 0.08$).

In general adults had lower fCORT concentrations in feathers grown after the 2013 breeding season than those grown after the 2012 season (ANOVA, Year: $F_{1,76} = 15.3449$, $p = 0.0002$, Fig. 2.4). However, changes in fCORT between years was not the same on all colonies (ANOVA, Year*Colony: $F_{2,76} = 12.4503$, $p < 0.0001$) because there was no difference in adult fCORT between years on St. Lazaria (Fig. 2.4). Feather CORT concentrations in adult feather tissues were positively correlated with fledgling fCORT concentrations on all three colonies in both years (Fig. 2.5).

Discussion

We examined how changes in diet during reproduction affected a piscivorous seabird breeding on three spatially distant colonies in the North Pacific. We found that intra-annual changes in diet occurred

on all three of our focal colonies, and that chick nutritional status (fCORT) and adult foraging behavior changed in tandem with prey species composition. Shifts in diet corresponded to changes in fCORT concentration in fledglings, which were mirrored in CORT concentrations in adult feathers grown after the breeding season. We acknowledge that the feathers used for CORT analysis may represent disproportionately high-quality chicks and adults that were able to survive to fledging age (chicks), and through the winter (adults). However, these individuals did exhibit changes in fCORT concentration both seasonally and inter-annually, thus it can be concluded that if our sampling were biased, the rest of the population may have been affected more severely by the diet changes we observed. Below we discuss one possible interpretation of these results.

When searching for food, predators may optimize prey mass, energy content, lipid content, and/or macronutrient availability (Kohl et al., 2015) depending on environmental conditions and an individual's needs (for e.g., in mammals see Gende et al., 2005). However, if prey quality is low, a predator may not have an optimal option. For example, in the North Sea common murres (*Uria aalge*) experienced reproductive failure when adults fed copious amounts of seabream (*Sprattus sprattus*) to their chicks when sand eels (*Ammodytes marinus*) were unavailable (Wanless et al., 2005). Such differences in energy content may be driven by lipid content, which is often correlated with the total energy in forage fish species (Van Pelt et al., 1997). For growing seabirds, lipids are critical to support growth and development; when absent, nestlings experience nutritional stress (Kitaysky et al., 2006, Romano et al., 2006). On Teuri we found that even a small reduction in the proportion of Japanese anchovy in RHAU chick diets corresponded to an increase in fCORT, suggesting that the moderate differences in prey energy content (Table 2.2) may have been compounded by differences in lipid content (Takahashi et al., 2001). While the quantity of fish delivered is often correlated with energy content we found that bill-load energy content was more strongly correlated to changes in fledgling fCORT concentrations.

On Middleton and St. Lazaria changes in diet composition between prey species equivalent in energy content also corresponded to changes in chick nutritional status (Fig. 2.2). In animals with parental care, adults act as an interface between foraging conditions and their young, and must balance their own energy intake while still providing for their offspring. This may result in adjustments to their daily delivery rate when prey becomes more or less available (Welham and Beauchamp, 1997); a response observed in many seabird species (e.g. Schrimpf et al., 2012, Kidawa et al., 2015, Hamer and Hill, 1993). Experimental work on Teuri indicated that reduced meal frequency negatively affects chick body condition (Takenaka et al., 2005). Thus meal delivery rate may explain some of the inter-annual variability in chick nutritional stress on the Alaskan colonies. On St. Lazaria, adult colony attendance, a proxy for delivery rate since RHAU return to the colony only once a day to feed their chick (Gaston and Dechesne, 1996), was low in 2012 compared to 2013, which corresponded to overall higher fledgling

fCORT in 2012. This suggests that RHAU reduce their meal delivery rate and prioritize self-maintenance over chick-provisioning, a decision which may affect their young.

How adult RHAU foraging behavior (putatively aimed at maximizing foraging efficiency) mediates the effects of foraging conditions on chick nutritional stress is less clear. In other alcids, an increase in foraging effort is characterized by an increase in time spent under the water (Young et al., 2015, Ronconi and Burger, 2008, Monaghan et al., 1994) and different diving patterns are associated with particular prey species (Elliott et al., 2008b). If that is the case it may be argued that some prey, such as Japanese anchovy, require more effort to obtain than others as Teuri adults engaged in longer bouts and dove deeper than birds on St. Lazaria in both years (Table 2.3). However, in 2013, when fCORT in fledglings was generally low, birds on both colonies spent more time underwater and engaged in more foraging bouts, suggesting greater foraging effort. It is possible that when prey quality increases, RHAU may be willing to expend more energy because the return on that energy is higher. Elliott et al. (2008a) found that the dive duration of thick-billed murres (*Uria lomvia*) increased with prey mass. On St. Lazaria RHAU captured longer (2013 mean = 96.72 ± 1.03 [SE] mm; 2012 mean = 90.07 ± 0.8 mm) and heavier (2013 mean = 6.4 ± 0.2 g; 2012 mean = 3.99 ± 0.16 g) prey in 2013 compared to 2012, suggesting that prey size may explain the counterintuitive increase in the number and duration of bouts when foraging conditions appeared to be good.

Fluctuations in fCORT concentrations indicate that RHAU chicks can be affected by short-term reductions in prey quality and changes in adult foraging behavior. Even brief exposure to elevated levels of CORT during development have been shown to result in changes in personality (Spencer and Verhulst, 2007), an increased stress response (Kitaysky et al., 2001b, Love and Williams, 2008), and reduced memory function (reviewed in Schoech et al., 2011, Kitaysky et al., 2006). Furthermore, short bouts of stress during development can result in reduced life expectancy (Boonekamp et al., 2014, Haussmann et al., 2003). Whether levels of stress associated with dietary changes affect post-fledging survival and population processes at our focal colonies, however, remains to be examined.

The fCORT concentrations we observed in RHAU adults correlated with fCORT in fledglings suggesting that adults are affected by dietary changes as well, perhaps due to reduced energy intake (adults and offspring feed on similar prey during chick-rearing, Ito et al., 2009, Hipfner et al., 2013). While more direct evidence is needed, this correlation suggests that adults incur stress during the breeding season, which carries-over to the post-breeding molt, a circumstance that would hold true whether or not birds successfully bred. RHAU undergo a simultaneous molt; they lose and regrow all of their flight feathers over a period of less than six weeks (Gaston and Dechesne, 1996). During this time their ability to capture prey is compromised and they may become vulnerable to food shortages and predation. To compensate for these drawbacks many bird species are highly flexible in whether and when they

commence feather loss and regrowth (Hahn et al., 1991). During post-breeding molt RHAU are no longer tied to their colony. Geolocators deployed on Teuri revealed that RHAU breeders rapidly relocated away from the colony to northern regions where autumn phytoplankton blooms provide a burst of productivity and abundant food resources (Takahashi et al., 2015). Potential flexibility in molt initiation and observations of post-breeding movement patterns suggest that adult fCORT (in this study the feather tip, grown first) may be a signal of breeding season experiences rather than a measure of conditions at the molting location.

Our study provides some support for the junk-food hypothesis and insight into how marine predators may be affected by changes in diet composition. We found that changes in diet composition occur at different temporal and spatial scales and clearly affected RHAU. Chicks are responsive to minor changes in diet composition, adult foraging behavior is flexible, and adults may carry a signature of exposure to stress during the breeding season into the post-reproductive period. This suggests that moderate changes in diet composition during the breeding season can affect seabird physiology and be detected in feathers. Thus fCORT can be an effective way of assessing foraging conditions experienced during the chick-rearing period. These findings also serve as a caution to the anthropogenic removal of forage fish biomass near seabird colonies (Essingtona et al., 2015, Cury et al., 2011), and illustrate that the effects of removal may not be detectable immediately with traditional monitoring methods (e.g. reproductive success or population trends). We conclude that RHAU, a bird arguably adapted to variable environmental conditions, might be affected by relatively minor dietary changes, and that foraging behavior and physiological responses to changes in prey composition should be considered when evaluating the effect of prey quality on seabirds and other marine predators.

Acknowledgements

We thank the North Pacific Research Board (this is publication number 564) for a Graduate Research Fellowship awarded to A. Will and for funding under the Gulf of Alaska Integrated Ecosystem Research Project (F4181-2). We also thank: the Alaska Maritime National Wildlife Refuge, USFWS, for logistical and field support; A. Hovis, A. Millay, K. Hall and USFWS crew members for assistance on St. Lazaria; Y. Suzuki, K. Hoshina, K. Uchida and J. Watanabe for their assistance on Teuri Is.; Ruokun Zhou for expertly running the HPLC-MS/MS analysis; and the Institute of Arctic Biology, University of Alaska Fairbanks, for summer support. Thanks as well to M. Benowitz-Fredericks, A. Springer, G. Breed and two anonymous reviewers for comments and edits that greatly improved this manuscript. All work was completed under USFWS permit #MB70337A-3, Alaska Department of Fish and Game permits: 12-046, 13-079, 14-109, and approval by the University of Alaska Fairbanks' Institutional Animal Care and Use Committee #251294. The authors have no conflicts of interest to declare. This project was made

possible primarily by the North Pacific Research Board and also by the Institute of Arctic Biology at the University of Alaska Fairbanks. North Pacific Research Board, (Grant/Award Number: 'GOAIERP: F4181-2','Graduate Research Fellowship') Institute of Arctic Biology, University of Alaska Fairbanks, (Grant/Award Number: 'Summer Research Grant').

References

ALVERSON, D. L. 1992. A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): The conflict arena. Reviews in Aquatic Sciences, 6, 203-256.

BARRETT, R. T., ERIKSTAD, K. E., SANDVIK, H., MYKSVOLL, M., JENNI-EIERMANN, S., KRISTENSEN, D. L., MOUM, T., REIERSTEN, T. K. & VIKEBØ, F. 2015. The stress hormone corticosterone in a marine top predator reflects short-term changes in food availability. Ecology and Evolution. doi: 10.1002/ece3.1438

BENOWITZ-FREDERICKS, Z. M., SHULTZ, M. T. & KITAYSKY, A. S. 2008. Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. Deep-Sea Research Part II: Topical Studies in Oceanography, 55, 1868-1876.

BOONEKAMP, J. J., MULDER, G. A., SALOMONS, H. M., DIJKSTRA, C. & VERHULST, S. 2014. Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in wild birds. Proceedings of the Royal Society B, 281.

BORTOLOTTI, G. R., MARCHANT, T. A., BLAS, J. & GERMAN, T. 2008. Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. Functional Ecology, 22, 494-500.

BURKE, C. M. & MONTEVECCHI, W. A. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. Journal of Zoology, 278, 354-361.

CURY, P. M., BOYD, I. L., BONHOMMEAU, S., ANKER-NILSSEN, T., CRAWFORD, R. J. M., FURNESS, R. W., MILLS, J. A., MURPHY, E. J., ÖSTERBLOM, H., PALECZNY, M., PIATT, J. F., ROUX, J.-P., SHANNON, L. & SYDEMAN, W. J. 2011. Global seabird response to forage fish depletion—one-third for the birds. Science, 334, 1703-1706.

DORRESTEIJN, I., KITAYSKY, A. S., BARGER, C., BENOWITZ-FREDERICKS, Z. M., BYRD, G. V., SHULTZ, M. & YOUNG, R. 2012. Climate affects food availability to planktivorous least auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea. Marine Ecology Progress Series, 454, 207-220.

ELLIOTT, K. H., DAVERON, G. & GASTON, A. J. 2008a. Time allocation by a deep-diving bird reflects prey type and energy gain. Animal Behaviour, 75, 1301-1310.

ELLIOTT, K. H., WOO, K., GASTON, A. J., BENVENUTI, S., DALL'ANTONIA, L. & DAVOREN, G. K. 2008b. Seabird foraging behaviour indicates prey type. Marine Ecology Progress Series, 354, 289–303.

ESSINGTONA, T. E., MORIARTYA, P. E., FROEHLICHA, H. E., HODGSONA, E. E., KOEHNA, L. E., OKENB, K. L., SIPLEA, M. C. & STAWITZB, C. C. 2015. Fishing amplifies forage fish population collapses. Proceedings of the National Academy of Sciences, doi/10.1073/pnas.1422020112.

GASTON, A. J. & DECHESNE, S. B. 1996. Rhinoceros Auklet (*Cerorhinca monocerata*). In: POOLE, A. (ed.) The Birds of North America Online. Ithaca, NY: Cornell Lab of Ornithology.

GENDE, S. M., QUINN, T. P. & WILLSON, M. F. 2005. Consumption choice by bears feeding on salmon. Oecologia, 2001, 372–382.

GRÉMILLET, D., PICHEGRU, L., KUNTZ, G., WOAKES, A. G., WILKINSON, S., CRAWFORD, R. J. M. & RYAN, P. G. 2008. A junk-food hypothesis for gannets feeding on fishery waste. Proceedings of the Royal Society B, 275, 1149-1156.

GRIFFITHS, R., DOUBLE, M. C., ORR, K. & DAWSON, R. J. G. 1998. A DNA test to sex most birds. Molecular Ecology, 7, 1071-1075.

HAHN, T. P., SWINGLE, J., WINGFIELD, J. C. & RAMENOFSKY, M. 1991. Adjustments of the prebasic molt schedule in birds. Ornis Scandinavica, 23, 314-321.

HAMER, K. C. & HILL, J. K. 1993. Variation and regulation of meal size and feeding frequency in Cory's shearwater *Calonectris diomedea*. Journal of Animal Ecology, 62, 441-450.

HARDING, A., PAREDES, R., SURYAN, R., ROBY, D., IRONS, D., ORBEN, R., RENNER, H., YOUNG, R., BARGER, C., DORRESTEIJN, I. & KITAYSKY, A. 2013. Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. Deep-Sea Research Part II: Topical Studies in Oceanography, 94, 178-191.

HARDING, A. M. A., KITAYSKY, A. S., HALL, M. E., WELCKER, J., KARNOVSKY, N. J., TALBOT, S. L., HAMER, K. C. & GRÉMILLET, D. 2009. Flexibility in the parental effort of an Arctic-breeding seabird. Functional Ecology, 23, 348-358.

HATCH, S. A. 2013. Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. Marine Ecology Progress Series, 477, 271–284.

HAUSSMANN, M. F., HUNTINGTON, C. E., WINKLER, D. W., NISBET, I. C. T., O'REILLY, K. M. & VLECK, C. M. 2003. Telomeres shorten more slowly in long-lived birds and mammals than in short-lived ones. The Royal Society, 270, 1387–1392.

HEDD, A., BERTRAM, D. F., RYDER, J. L. & JONES, I. L. 2006. Effects of interdecadal climate variability on marine trophic interactions: rhinoceros auklets and their fish prey. Marine Ecology Progress Series, 309, 263-278.

HEDD, A., REGULAR, P. M., MONTEVECCHI, W. A., BUREN, A. D., BURKE, C. M. & FIFIELD, D. A. 2009. Going deep: common murres dive into frigid water for aggregated, persistent and slow-moving capelin. Marine Biology, 156, 741-751.

HIPFNER, J. M., MCFARLANE-TRANQUILLA, L., ADDISON, B. & HOBSON, K. A. 2013. Trophic responses to the hatching of offspring in a central-place foraging seabird. Journal of Ornithology, 154, 965-970.

HIROSE, F., KAZAMA, K., ITO, M. & WATANUKI, Y. 2012. Accelerated growth rates in late-hatched Rhinoceros Auklet *Cerorhinca monocerata* chicks depend on food conditions and growth stage: an experimental approach. Ibis, 154, 296,306.

HJERNQUIST, B. & HJERNQUIST, MÅRTEN B. 2010. The effects of quantity and quality of prey on population fluctuations in three seabird species. Bird Study, 57, 19-25.

HOVIS, A. & SLATER, L. 2012. Biological Monitoring at St. Lazaria Island, Alaska, in 2012. In: USFWS (ed.) AMNWR 13/06 ed. Homer Alaska.

ITO, M., MINAMI, H., TANAKA, Y. & WATANUKI, Y. 2009. Seasonal and inter-annual oceanographic changes induce diet switching in a piscivorous seabird. Marine Ecology Progress Series, 393, 273-284.

ITO, M., TAKAHASHI, A., KOKUBUN, N., KITAYSKY, A. S. & WATANUKI, Y. 2010. Foraging behavior of incubating and chick-rearing thick-billed murres *Uria lomvia*. Aquatic Biology, 8, 279-287.

JACKSON, A. C. & RUNDLE, S. D. 2008. Diet-shifts by an estuarine goby (*Pomatoschistus microps*) in the face of variable prey availability. Journal of Experimental Marine Biology and Ecology, 361, 1-7.

JODICE, P. G. R., ROBY, D. D., TURCO, K. R., SURYAN, R. M., IRONS, D. B., PIATT, J. F., SHULTZ, M. T., ROSENEAU, D. G., KETTLE, A. B. & ANTHONY, J. A. 2006. Assessing the nutritional stress hypothesis: relative influence of diet quantity and quality on seabird productivity. Marine Ecology Progress Series, 325.

KADIN, M., ÖSTERBLOM, H., HENTATI-SUNDBERG, J. & OLSSON, O. 2012. Contrasting effects of food quality and quantity on a marine top predator. Marine Ecology Progress Series, 444, 239-249.

KARNOVSKY, N. J., BROWN, Z. W., WELCKER, J., HARDING, A. M. A., WALKUSZ, W., CAVALCANTI, A., HARDIN, J., KITAYSKY, A., GABRIELSEN, G. & GRÉMILLET, D.

2011. Inter-colony comparison of diving behavior of an Arctic top predator: implications for warming in the Greenland Sea. Marine Ecology Progress Series, 440, 229-240.

KIDAWA, D., JAKUBASA, D., WOJCZULANIS-JAKUBASA, K., STEMPNIEWICZA, L., TRUDNOWSKAB, E., BOEHNKEB, R., KESLINKA-NAWROTAC, L. & BŁACHOWIAK-SAMOŁYKB, K. 2015. Parental efforts of an Arctic seabird, the little auk *Alle alle*, under variable foraging conditions. Marine Biology Research, 11, 349-360.

KIKUCHI, D. M., WATANUKI, Y., SATO, N., HOSHINA, K., TAKAHASHI, A. & WATANABE, Y. Y. 2015. Strouhal number for flying and swimming in rhinoceros auklets *Cerorhinca monocerata*. Journal of Avian Biology, 46, 001-006.

KITAYSKY, A., KITAISKAIA, E. V., PIATT, J. F. & WINGFIELD, J. C. 2006. A mechanistic link between chick diet and decline in seabirds? Proceedings of the Royal Society B, 273, 445-450.

KITAYSKY, A., WINGFIELD, J. C. & PIATT, J. F. 2001a. Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. Behavioral Ecology, 12, 619-625.

KITAYSKY, A. S., KITAISKAIA, E. V., PIATT, J. F. & WINGFIELD, J. C. 2003. Benefits and costs of increased levels of corticosterone in seabird chicks. Hormones and Behavior, 43, 140-149.

KITAYSKY, A. S., KITAISKAIA, E. V., WINGFIELD, J. C. & PIATT, J. F. 2001b. Dietary restriction causes chronic elevation of corticosterone and enhances stress response in red-legged kittiwake chicks. Journal of Comparative Physiology B, 171, 701-709.

KITAYSKY, A. S., PIATT, J. F., BENOWITZ-FREDERICKS, Z. M., HATCH, S. A., SHULTZ, M. T., KITAISKAIA, E. V. & WINGFIELD, J. C. 2010. Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Functional Ecology, 24, 625-637.

KITAYSKY, A. S., WINGFIELD, J. C. & PIATT, J. F. 1999. Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. Functional Ecology, 13, 577-584.

KOHL, K. D., COOGAN , S. C. P. & RAUBENHEIMER, D. 2015. Do wild carnivores forage for prey or for nutrients? Bioessays, 37, DOI 10.1002/bies.201400171.

KOREN, L., NG, E. S. M., SOMA, K. K. & WYNNE-EDWARDS, K. E. 2012. Sample preparation and liquid chromatography-tandem mass spectrometry for multiple steroids in mammalian and avian circulation. PLoS ONE, 7, e32496.

LOVE, O. P. & WILLIAMS, T. D. 2008. Plasticity in the adrenocortical response of a free-living vertebrate: The role of pre- and post-natal developmental stress. Hormones and Behavior, 54, 496-505.

MOLEÓN, M., SÁNCHEZ-ZAPATA, J. A., REAL, J., GARCIA-CHARTON, J. A., GIL-SÁNCHEZ, J. M., PALMA, L., BAUTISTA, J. & BAYLE, P. 2009. Large-scale spatio-temporal shifts in the diet of a predator mediated by an emerging infectious disease of its main prey. Journal of Biogeography, 36, 1502-1515.

MONAGHAN, P., WALTON, P., WANLESS, S., UTTLEY, J. D. & BURNS, M. D. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. Ibis, 136, 214-222.

NIIZUMA, Y., TAKAHASHI, A., KUROKI, M. & WATANUKI, Y. 1999. Sexing by external measurements of adult rhinoceros auklets breeding on Teuri Island. Japan Journal of Ornithology, 48, 145-150.

RECTOR, M. E., KOUWENBERG, A. L., WILHELM, S. J., ROBERTSON, G. J., MCKAY, D. W., FITZSIMMONS, M. G., BAKER, C. R., CAMERON-MACMILLAN, M. L., WALSH, C. J. & STOREY, A. E. 2012. Corticosterone levels of Atlantic puffins vary with breeding stage and sex but are not elevated in poor foraging years. General and Comparative Endocrinology, 178, 408-416.

ROMANO, M. D., PIATT, J. F. & ROBY, D. D. 2006. Testing the Junk-food Hypothesis on Marine Birds: Effects of Prey Type on Growth and Development. Waterbirds, 29, 407-524.

RONCONI, R. A. & BURGER, A. E. 2008. Limited foraging flexibility: increased foraging effort by a marine predator does not buffer against scarce prey. Marine Ecology Progress Series, 366, 245-258.

SCHOECH, S. J., RENSEL, M. A. & HEISS, R. S. 2011. Short- and long-term effects of developmental corticosterone exposure on avian physiology, behavioral phenotype, cognition, and fitness: A review. Current Zoology, 57, 514-530.

SCHRIMPF, M. B., PARRISH, J. K. & PEARSON, S. F. 2012. Trade-offs in prey quality and quantity revealed through the behavioral compensation of breeding seabirds. Marine Ecology Progress Series, 460, 247-259.

SEARS, J. & HATCH, S. A. 2008. Rhinoceros auklet developmental responses to food limitation: an experimental study. The Condor, 110, 709-717.

SIBLY, R. M., NOTT, H. M. R. & FLETCHER, D. J. 1990. Splitting behaviour into bouts. Animal Behaviour, 39, 63-69.

SIDDON, E. C., HEINTZ, R. A. & MUETER, F. J. 2013. Conceptual model of energy allocation in walleye pollock (*Theragra chalcogramma*) from age-0 to age-1 in the southeastern Bering Sea. Deep-Sea Research II, 94, 140-149.

SLATER, L. & BYRD, G. V. 2009. Status, trends, and patterns of covariation of breeding seabirds at St Lazaria Island, Southeast Alaska, 1994-2006. Journal of Biogeography, 36, 465-475.

SPENCER, K. A. & VERHULST, S. 2007. Delayed behavioral effects of postnatal exposure to corticosterone in the zebra finch (*Taeniopygia guttata*). Hormones and Behavior, 51, 23-280.

SVANBÄCK, R. & BOLNICK, D. I. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B, 274, 839-844.

TAKAHASHI, A., ITO, M., SUZUKI, Y., WATANUKI, Y., THIEBOT, J.-B., YAMAMOTO, T., IIDA, T., TRATHAN, P., NIIZUMA, Y. & KUWAE, T. 2015. Migratory movements of rhinoceros auklets in the northwestern Pacific: connecting seasonal productivities. Marine Ecology Progress Series, 525, 229-243.

TAKAHASHI, A., KUROKI, M., NIIZUMA, Y., KATO, A., S, S. & WATANUKI, Y. 2001. Importance of Japanese anchovy (*Engraulis japonicus*) to breeding rhinoceros auklets (*Cerorhinca monocerata*) on Teuri Island, Sea of Japan. Marine Biology, 139, 361-371.

TAKENAKA, M., NIIZUMA, Y. & WATANUKI, Y. 2005. Resource allocation in fledglings of the rhinoceros auklet under different feeding conditions: an experiment manipulating meal size and frequency. Canadian Journal of Zoology, 83, 1476-1485.

THOMPSON, C. W. & KITAYSKY, A. S. 2004. Polymorphic flight-feather molt sequence in tufted puffins (*Fratercula cirrhata*): A rare phenomenon in birds. The Auk, 121, 35-45.

VAN PELT, T. I., PIATT, J. F., LANCE, B. K. & ROBY, D. D. 1997. Proximate composition and energy density of some North Pacific forage fishes. Comparative Biochemical Physiology, 118A, 1393-1398.

WANLESS, S., FREDERIKSEN, M., DAUNT, F., SCOTT, B. E. & HARRIS, M. P. 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. Progress in Oceanography, 72, 30-38.

WANLESS, S., HARRIS, M. P., REDMAN, P. & SPEAKMAN, J. R. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Marine Ecology Progress Series, 294, 1-8.

WATANUKI, Y. & ITO, M. 2012. Climatic effects on breeding seabirds of the northern Japan Sea. Marine Ecology Progress Series, 454, 183-196.

WATANUKI, Y., ITO, M., DEGUCHI, T. & MINOBE, S. 2009. Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. Marine Ecology Progress Series, 393, 259-271.

WELHAM, C. V. J. & BEAUCHAMP, G. 1997. Parental provisioning in a variable environment: Evaluation of three foraging currencies and a state variable model. Evolutionary Ecology, 11, 399-417.

WILL, A. P., SUZUKI, Y., ELLIOTT, K. H., HATCH, S. A., WATANUKI, Y. & KITAYSKY, A. S. 2014. Feather corticosterone reveals developmental stress in seabirds. The Journal of Experimental Biology, 217, 2371-2376.

WINGFIELD, J. C. & FARNER, D. S. 1975. The determination of five steroids in avian plasma by radioimmunoassay and competitive protein-binding. Steroids, 26, 311-327.

YOUNG, R. C., KITAYSKY, A. S., BARGER, C. P., DORRESTEIJN, I., ITO, M. & WATANUKI, Y. 2015. Telomere length is a strong predictor of foraging behavior in a long-lived seabird. Ecosphere, 6:39.

ZHOU, Y., CHEN, W., KANEKO, Y., NEWMAN, C., LIAO, Z., ZHU, X., BUESCHING, C. D., XIE, Z. & MACDONALD, D. W. 2015. Seasonal dietary shifts and food resource exploitation by the hog badger (*Arctonyx collaris*) in a Chinese subtropical forest. European Journal of Wildlife Research, 61, 125-133.

Figures

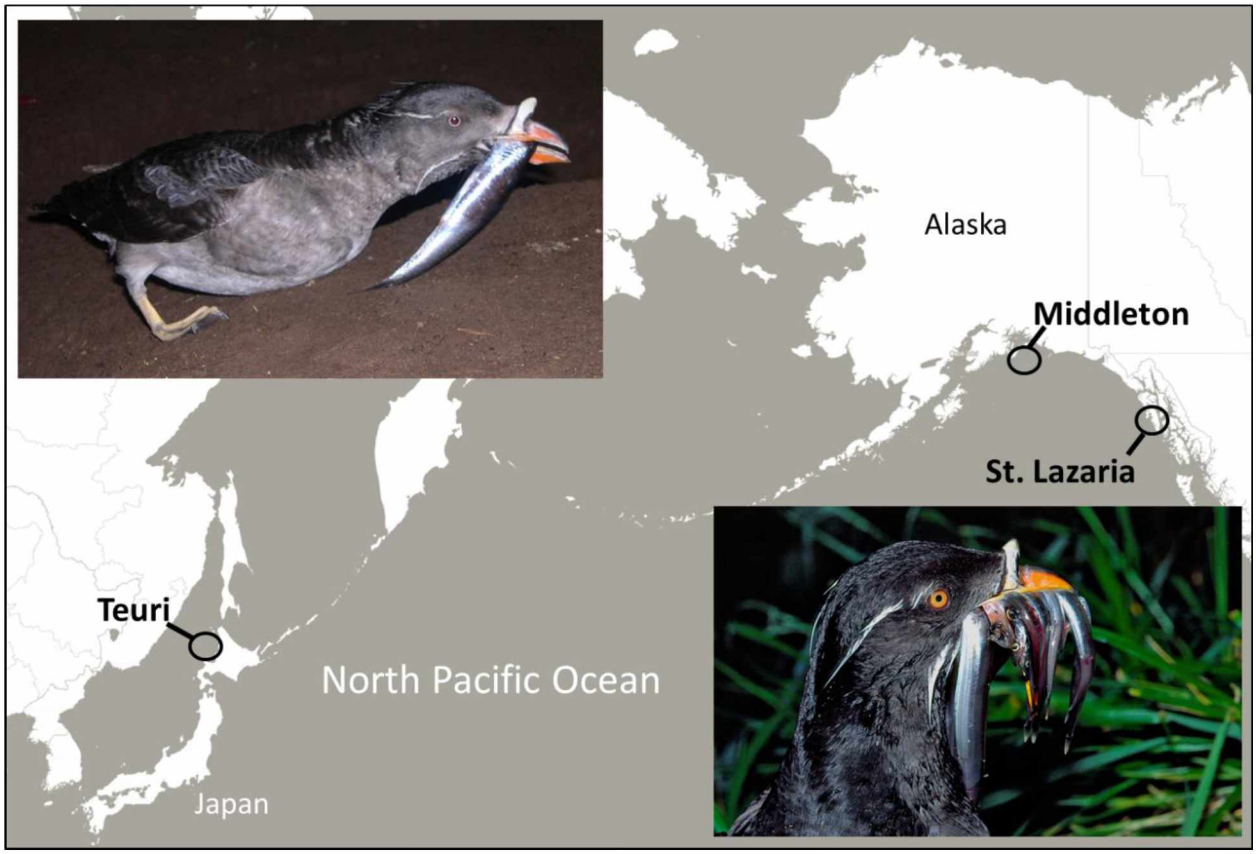

Figure 2.1 The rhinoceros auklet and field sites. Photos are of rhinoceros auklets returning to their colonies at night with a "bill load" of fish for their chicks on Teuri Is. by Motohiro Ito (top left) and on Chowiet Is., Gulf of Alaska, by Nikolai Konyukhov (bottom right). Base map from Stamen Maps.

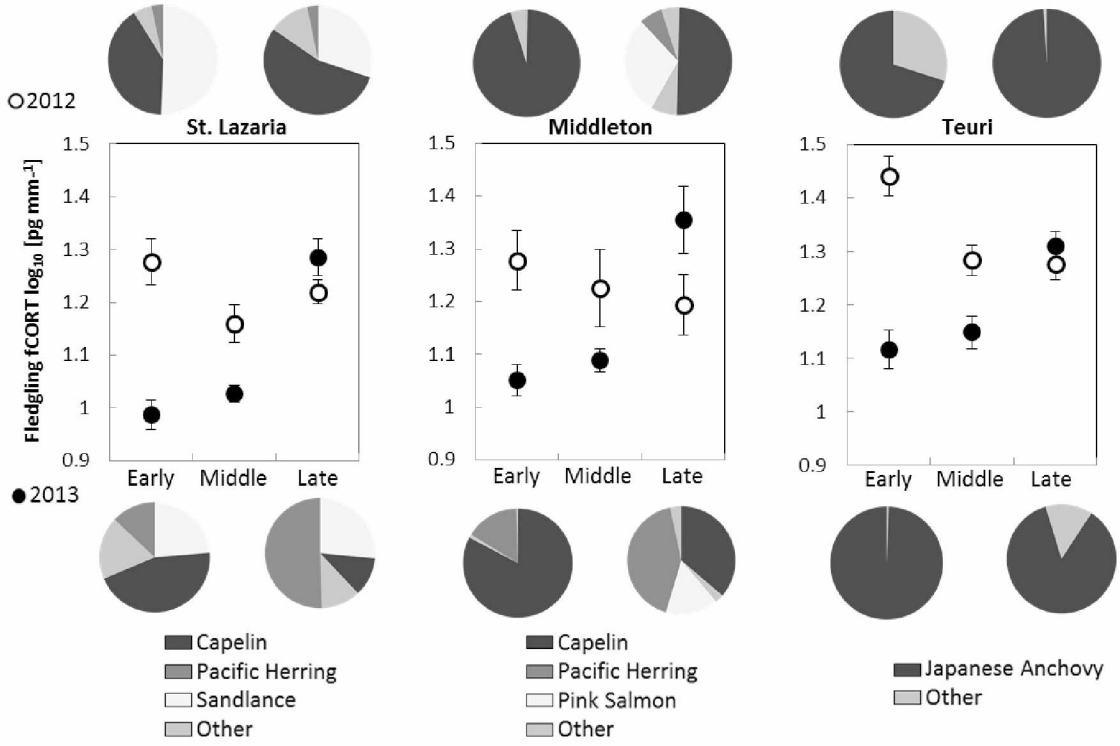

Figure 2.2 Temporal and spatial changes in diet composition and nutritional stress incurred by RHAU chicks. Log transformed fCORT concentrations measured in primaries of free-living RHAU fledglings on St Lazaria (2012 n = 13; 2013 n = 14), Middleton (2012 n = 6; 2013 n = 7), and Teuri (2012 n = 15; 2013 n = 16) islands. Feather segments: Early = tip, Middle = middle, and Late = base of the feather ± SE. The pie charts illustrate bill load composition delivered during the first and second half of the breeding season. Proportions are of total energy delivered (kJ g^{-1}, wet mass) per prey type.

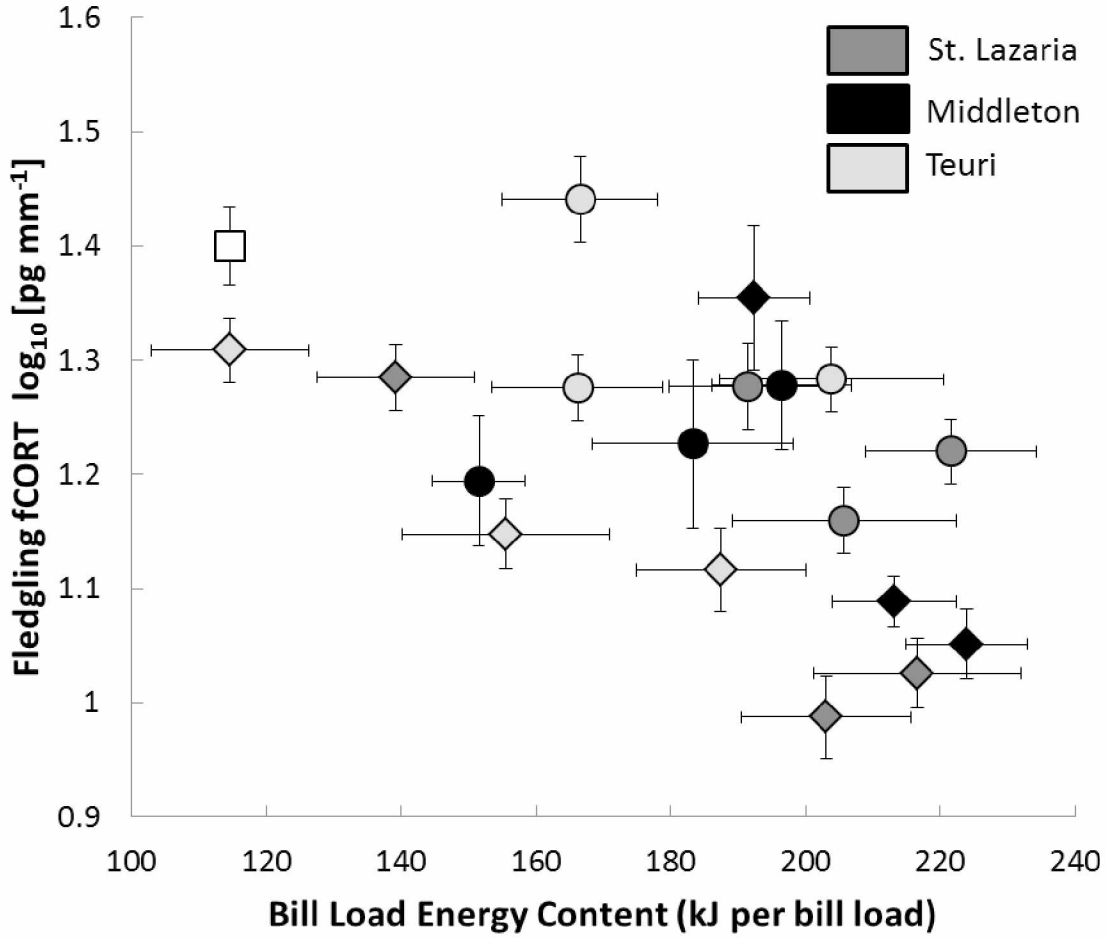

Figure 2.3 Bill load energy content and fCORT. Mean bill load energy (± SE) in diet samples collected at St. Lazaria, Middleton, and Teuri during early, middle, and late feather growth periods in 2012 (circles) and 2013 (diamonds). We compared these colony-wide values to the average fCORT concentrations (± SE) of feather segments sampled from fledglings. (□) is the mean (± SE) fCORT concentration of captive-reared chicks on a restricted diet (239 kJ day^{-1} or ~114 kJ per "parent"; Will et al., 2014) and is shown for comparative purposes.

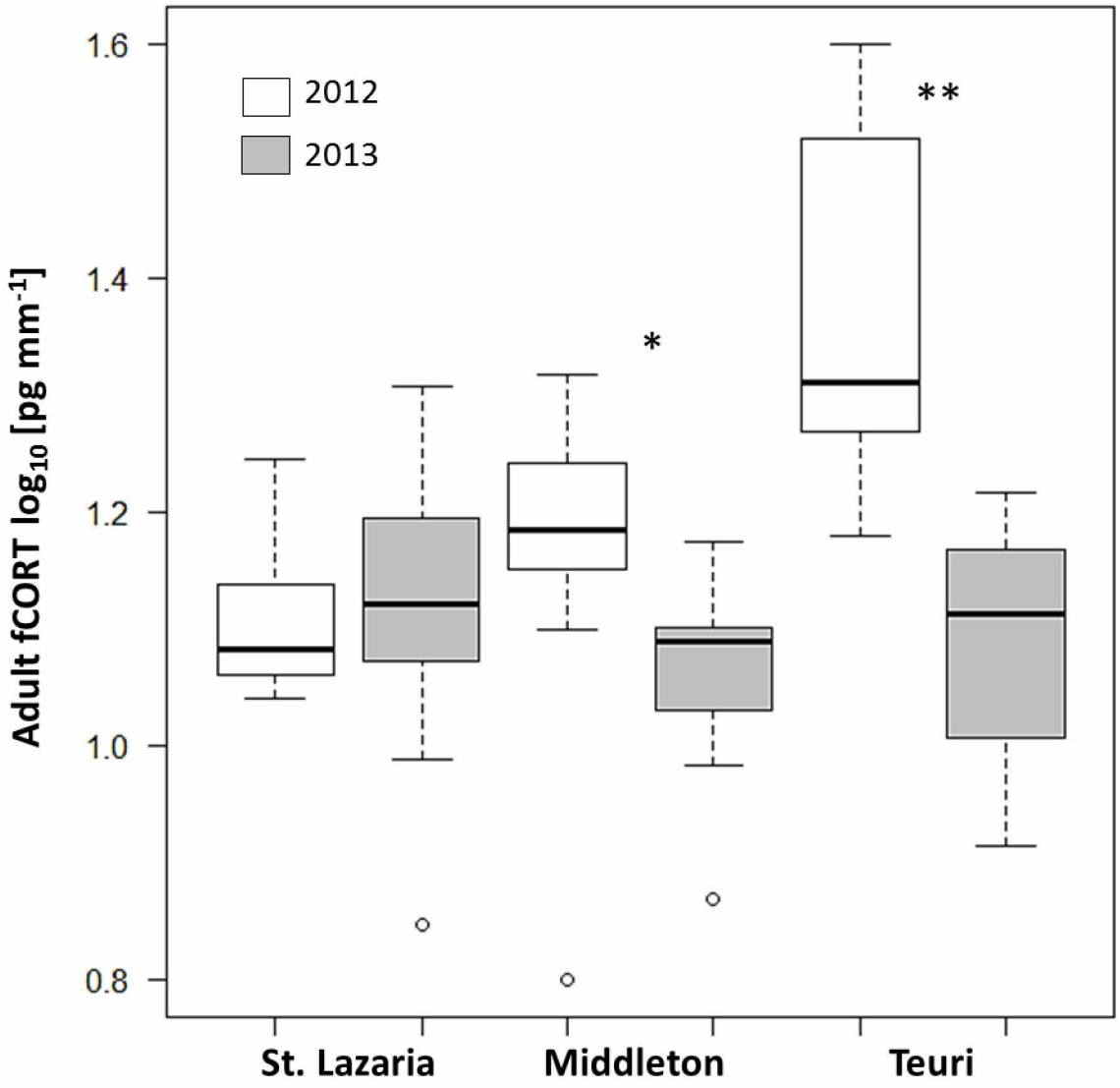

Figure 2.4 Feather CORT concentrations in adult feather tips. Median fCORT concentrations (solid line) shown in relation to the distribution of values for adults sampled on St. Lazaria (2012 n = 17; 2013 n = 19), Middleton (2012 n = 14; 2013 n = 15), and Teuri (2012 n = 7; 2013 n = 10). The distribution of adult fCORT concentrations are illustrated with boxes (middle 50 %) ± whiskers (the outer 25 %), and open circle "outliers" (no values were excluded from analysis). 2012 and 2013 refer to the year in which the feathers were grown; birds were sampled during the following breeding season. * $p < 0.01$, ** $p < 0.001$.

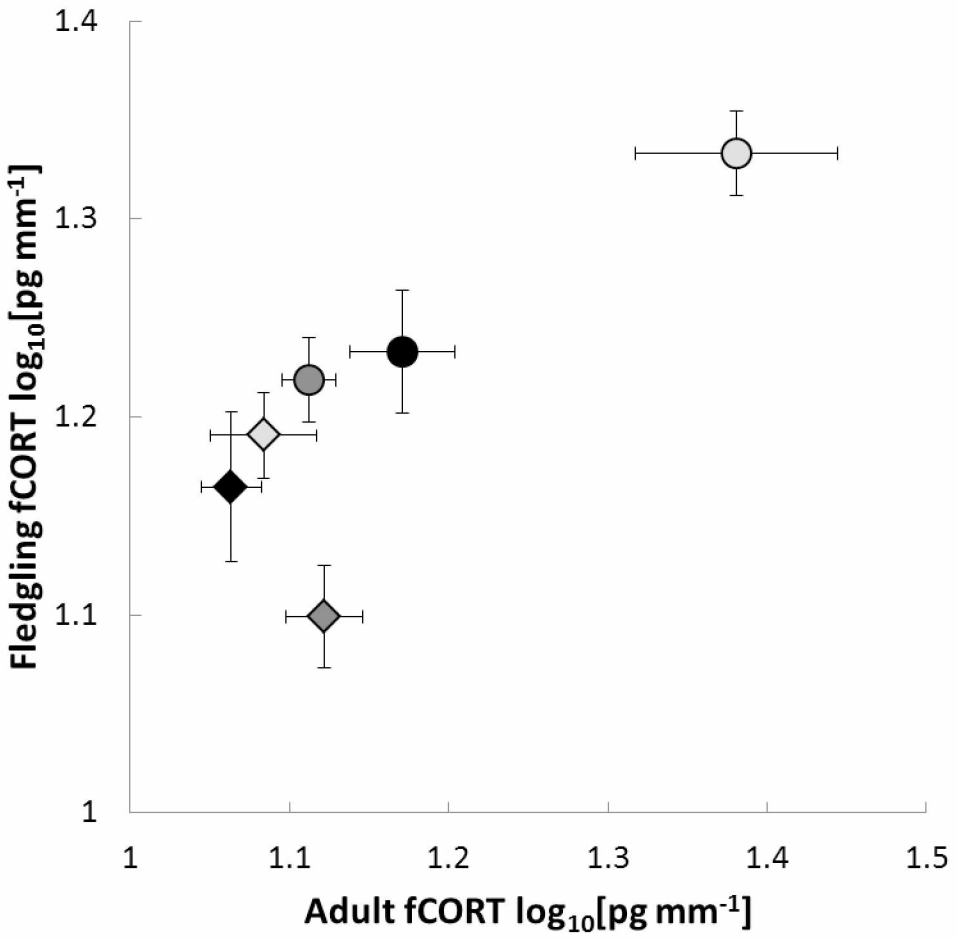

Figure 2.5 CORT concentrations in post-reproductive adult feathers correlate with CORT concentrations in fledgling feathers. Plotted are the average CORT concentrations measured in the tip (25 mm) of adult feathers and 20 mm segments of fledgling feathers for St. Lazaria, Middleton, and Teuri Islands for the 2012 (circles) and 2013 (diamonds) post-reproductive (adults) and breeding (fledglings) seasons. Error bars are ± SE of the mean, adjusted-R^2 = 0.58, p = 0.048.

Tables

Table 2.1 Prey composition of RHAU bill loads. Percent of energy attributed to prey species in RHAU bill loads collected on St. Lazaria, Middleton, and Teuri Islands. "Early" refers to the first half of the chick-rearing period, and "Late" to the second half (see Methods for details). The number of bill loads collected in each period is listed in parentheses and the primary prey species for each colony is highlighted in bold.

		2012		2013	
		% Early	% Late	%Early	% Late
St. Lazaria		(n = 38)	(n = 41)	(n = 50)	(n = 47)
	Capelin	40.57	54.48	44.97	11.42
	Pacific Sandlance (A. hexapterus)	50.58	30.1	23.67	26.56
	Pacific Herring	3.4	3.27	12.95	50.36
	Greenling spp	2.53	8.28	16.98	9.33
	Salmon spp	2.92	3.87	1.43	2.33
Middleton		(n = 99)	(n = 113)	(n = 109)	(n = 82)
	Capelin	94.7	50	82.74	36.22
	Pink Salmon	2.4	29.9	0.68	15.82
	Pacific Herring	0.06	7	15.78	42
	Greenling spp	1.8	5.7	0.32	0.89
	Chum Salmon	0.3	0	0	3.38
	Other	0.74	7.4	0.48	1.69
Teuri		(n = 30)	(n = 59)	(n = 50)	(n = 40)
	Japanese Anchovy	70	99	99.4	86.1
	Japanese Greenling	15.6	0	0.2	0
	Sandlance +1 (A. personatus)	8.6	0	0.4	4.2
	Sandlance 0 (A. personatus)	0	1	0	8.4
	Other	5.8	0	0	1.3

Table 2.2 Energy content of RHAU prey species. Energy content is measured as kJ g^{-1} wet mass and was derived from: 1) analysis of prey from St. Lazaria RHAU bill loads in 2012 and 2013 (see Methods) and 2) "Published," Takahashi et al. (2001). Means are ± SE. Differences in Pacific sand lance (*A. hexapterus*) energy content were largely driven by fish size/age-class, RHAU adults delivered age-0 sand lance in 2012 and in 2013 they delivered age-1+.

	Energy Content									
	2012		**n**	**2013**		**n**	**t-test**	**Published**		**n**
Capelin	6.96	± 0.21	(8)	6.97	± 0.32	(8)	0.48			
Pacific Sand lance (A. hexapterus)	6.39	± 0.22	(8)	6.96	± 0.20	(8)	0.07			
Pacific Herring				5.97	± 0.13	(8)				
Greenling spp	5.75	± 0.13	(8)	5.63	± 0.20	(8)	0.3			
Pink Salmon	4.53	± 0.12	(5)	4.95	± 0.17	(3)	0.05			
Chum Salmon	4.38	± 0.15	(3)	4.55	± 0.18	(5)	0.27			
Japanese Anchovy								6.29	± 1.47	(6)
Japanese Greenling								4.78	± 0.63	(6)
Sand lance +1 (A. personatus)								5.47	± 1.93	(3)
Sand lance 0 (A. personatus)								3.78	± 0.44	(3)

Table 2.3 Summary of diving parameters for chick-rearing RHAU on St. Lazaria Island (2012, 11 birds and 36 bird days; 2013, 20 birds and 78 bird days) and Teuri Island (2012, 8 birds and 8 bird days; 2013, 8 birds and 11.5 bird days). Sample sizes (n) appear in parentheses above the means ± SE.

	St. Lazaria		Teuri			p-value		
	2012	2013	2012	2013	Model	Year	Colony	Year*Colony
Bout-based Parameters	(n = 878)	(n = 2779)	(n = 140)	(n = 267)				
Dives per Bout	11.09 ± 0.60	9.76 ± 0.34	9.02 ± 0.84	8.04 ± 0.67	GLMM negative binomial	0.38	0.25	0.89
Bout Duration (sec)	374.09 ± 23.25	391.57 ± 13.83	618.82 ± 66.66	593.37 ± 48.77	GLMM negative binomial	0.63	0.04	0.89
Average Bout Depth (m)	4.42 ± 0.15	4.39 ± 0.10	13.69 ± 0.91	15.54 ± 0.70	GLMM Poisson	0.84	<0.001	0.62
Bird-based Parameters	(n = 36)	(n = 78)	(n = 8)	(n = 11.5)				
Bouts per Day	24.39 ± 1.19	35.63 ± 1.43	17.50 ± 2.14	23.75 ± 2.32	LME	<0.001	0.003	0.41
Time Underwater per Day (square-root sec)	74.49 ± 3.17	96.24 ± 2.68	84.03 ± 9.19	101.10 ± 7.06	LME	0.003	0.54	0.77

Appendix 2.A: Molecular Validation

To identify whether rhinoceros auklet chicks and adults have corticosterone in their feathers we followed the high-performance liquid chromatography tandem mass-spectrometry (LC-APCI/MRM/MS) approach (Koren et al. 2012; Keevil 2013).

Methods

Chemicals and Reagents

HPLC-grade standard corticosterone was purchased from Steroids Inc. (Newport, Rhode Island, USA). Deuterium-labeled internal standard, corticosterone-2,2,4,6,6,17α,21,21-d8 (corticosterone-d8), was obtained from CDN Isotopes Inc. (Pointe-Claire, Quebec, Canada). HPLC-grade methanol was purchased from Fisher Scientific (Edmonton, Alberta, Canada). Deionized water was prepared by Barnstead E-PURE Water System (Dubuque, Iowa, USA). LC-MS nitrogen was generated by a Source5000 nitrogen generator (Parker Balston, Haverville, Massachusetts, USA).

Sample Extraction Procedure

A standard solution or feather sample was placed in a 13 × 100 mm culture test tube, and 100 μL of deuterium-labeled internal standard solution and 9 mL cold methanol were added. The test tube was capped and stored in a 4°C fridge for 20 hours. After the feather was removed from the test tube, the extract was evaporated to dryness under nitrogen at 40°C by use of Techne Sample Concentrator and reconstituted with 200 μL of acetonitrile:H_2O (50/50, v/v). The sample was centrifuged at 14,000 rpm (Legend micro-21R, Thermo Scientific) for 20 minutes and 150 μL of its supernatant was submitted to LC-MS.

LC-APCI/MRM/MS Analysis

Extracts of two feather samples (one from an adult and one from a fledging) were analyzed by using an Agilent 1200 binary liquid chromatography (LC) system connected with an AB SCIEX QTRAP® 5500 tandem mass spectrometer equipped with an atmospheric pressure chemical ionization (APCI) source. LC separation was performed on an Agilent Poroshell 120 C18 column (50 x 3 mm, 2.7 μm particle size) at 45°C. The mobile phase A was H_2O/MeOH (75/25, v/v) and the mobile phase B was 100% methanol. The 8.5 min gradient was 20-50% B (0-1.0 min), 50-70% B (1.0-5.0 min), 70-100% B (5.0-5.5 min), 100-100% B (5.5-6.5 min), 100-20% B (6.5-7.0 min), and held at 20% B (7.0-8.5 min). The flow rate was 0.6 mL/min and the injection volume was 15 μL.

The analytes were ionized under positive APCI mode and the data were acquired via multiple reaction monitoring (MRM). Mass spectrometer conditions are listed in Table 2.A-1. Mass resolutions in

Q1 and Q3 were set to unit resolution. Each analyte was monitored by two transitions (a quantifier and a qualifier) with conditions listed in Table 2.A-2.

Calibration Curve and Lower Limit of Quantification

Calibrant solutions were prepared by diluting the stock solution with water as shown in Table 3. Lower limit of quantification (LLOQ) of each steroid was defined by a statistical analysis.[3] Details of the testing results are available as an .xlsx file, on request.

Table 2.A-1 Mass spectrometer conditions

Parameter	**Value**
Curtain gas	35 psi
Temperature	600 °C
Ion Source Gas 1	35 psi
Ion Source Gas 2	60 psi
Collision Gas	Medium
Nebulizer Current	5 μA

Table 2.A-2 MRM conditions for the steroids analyzed in APCI positive mode. (DP= declustering potential, EP= entrance potential, CE= collision energy, and CXP= collision cell exit potential).

Analyte	**MRM Transitions**	**DP (V)**	**EP (V)**	**CE (eV)**	**CXP (V)**
Corticosterone	347/329 347/121	80	10	24	12
Corticosterone-d8	355/337 355/125	80	10	24	12

([3]) http://www.absciex.com/Documents/Downloads/Literature/mass-spectrometry-cms_059150.pdf

Table 2.A-3 Concentrations (ng/mL) of calibrators prepared in Methanol:H_2O (50/50, v/v).[4]

Compound	STD 1	STD 2	STD 3	STD 4	STD 5	STD 6	STD 7	STD 8
Corticosterone	20	10	4	2	1	0.4	0.2	0.1

Table 2.A-4 Raw data acquired by QTRAP5500.

Sample Name	corticosterone (ng/mL)
Cal 8	0.12
Cal 7	0.18
Cal 6	0.40
Cal 5	1.04
Cal 4	1.79
Cal 3	3.95
Cal 2	9.36
Cal 1	20.87
Adult feather	0.13
Fledging feather	0.21

Results

Corticosterone was detectable (intensity higher than LLOQ) in adult and fledgling feather tissues. Retention time was 2:51 (min:sec) and concentrations for the calibration curve and feather samples are reported in Table 3.4. Chromatograms for counts per second (cps) of the corticosterone ion are shown in Figures 2.A-1 (adult) and 2.A-2 (fledgling).

([4]) R^2 of the calibration curve is greater than 0.99.

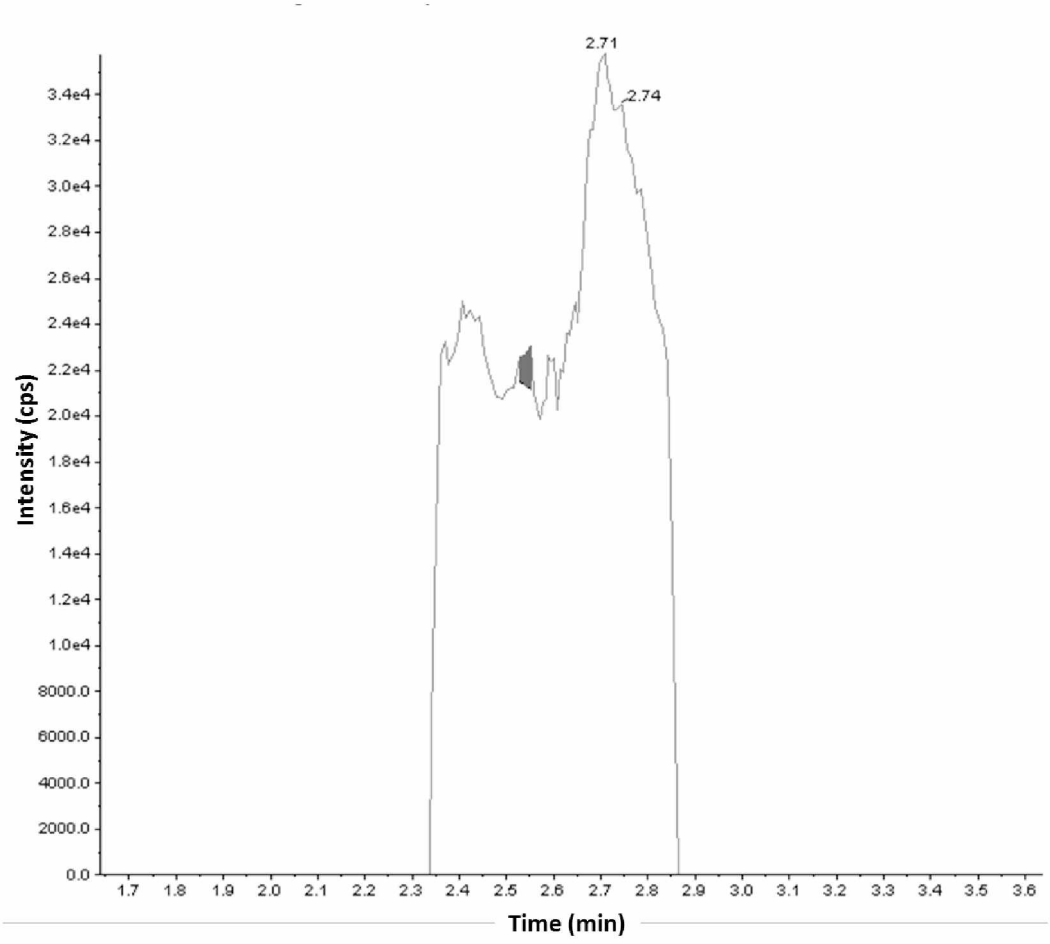

Figure 2.A-1 Chromatogram for corticosterone concentration in the first primary feather of an adult rhinoceros auklet. The shaded peak indicates the concentration of corticosterone present in the sample.

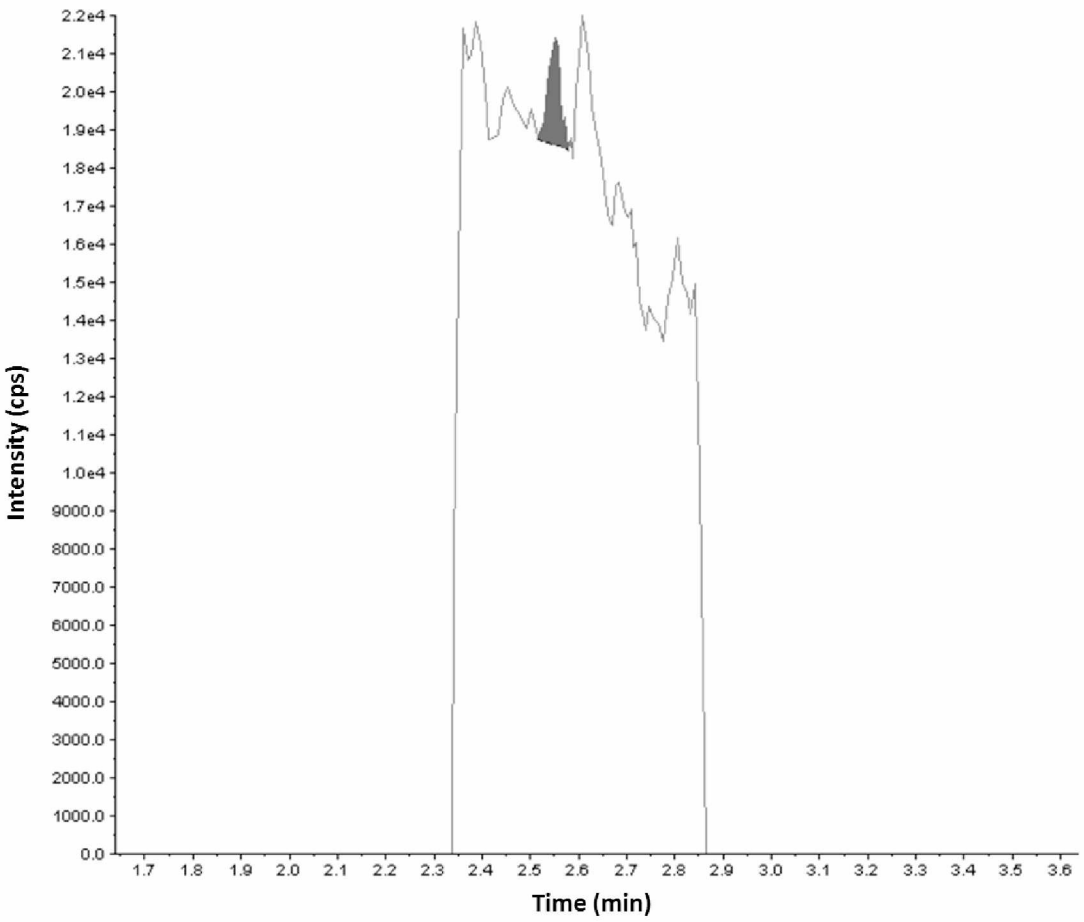

Figure 2.A-2 Chromatogram for corticosterone concentration in the first primary feather of a rhinoceros auklet fledgling. The shaded peak indicates the concentration of corticosterone present in the sample.

References

KEEVIL, B.G. (2013) Novel liquid chromatography tandem mass spectrometry (LC-MS/MS) methods for measuring steroids. Best Practice & Research Clinical Endocrinology & Metabolism, 27, 663-674.

KOREN, L., MAKAGAWA, S., BURKE, T., SOMA, K.K., WYNNE-EDWARDS, K.E. & GREFFEN, E. (2012) Non- breeding feather concentrations of testosterone, corticosterone and cortisol are associated with subsequent survival in wild house sparrows. Proc Biol Sci, 279, 1560-1566.

Chapter 3 Variability in Trophic Level and Habitat Use in Response to Environmental Forcing: Isotopic Niche Dynamics of Breeding Seabirds in the Southeastern Bering Sea[5].

Abstract

Climate driven changes in the marine environment may affect inter- and intraspecific resource partitioning by marine organisms. When and how resources are partitioned may also depend on the diversity of foraging habitat types. Previous studies have found that changes in diet and habitat use are reflected in an animal's isotopic niche.

Here we examined the variability in the isotopic niche of breeding seabirds in cold compared to warm temperature states in the Bering Sea and with respect to access to different types of foraging habitat. Between 1999 and 2015 (n = 12 years) we collected blood from black-legged kittiwakes ("kittiwakes", *Rissa tridactyla*), and common (*Uria aalge*) and thick-billed murres (*U. lomvia*) breeding on St. George and St. Paul Islands on the southeastern Bering Sea continental shelf. We examined isotopic niche dynamics at the group and species levels.

Stable isotope signatures of blood tissues corroborated independent observations of seabird distributions in the region. All three species increased foraging on shelf-based (enriched in $\delta^{13}C$) prey during warm oceanographic conditions, in contrast to a higher reliance on oceanic-based prey (depleted in $\delta^{13}C$) during cold conditions. Under warm conditions, the isotopic niche of the seabird group with access to only shelf habitat (St. Paul Island) contracted, whereas the isotopic niche of the seabird group with access to shelf, slope, and basin habitats (St. George Island) expanded. Patterns of prey availability in the region indicated that prey for breeding murres and kittiwakes became more available on the continental shelf adjacent to the breeding colonies during warm conditions, suggesting group-level responses were associated with increased food availability. At the species level, isotopic niches expanded over the course of the breeding season (from arrival to chick-rearing) on both colonies independent of oceanographic conditions, suggesting that either prey diversified over the course of the season and/or that individuals engaged in a broader variety of foraging specialization. We conclude that habitat heterogeneity in the vicinity of breeding colonies may mediate how predators partition food resources in response to changes in climate-driven food availability.

[5] Will, Alexis; Kitaysky, Alexander. In preparation for Marine Ecology Progress Series: Special Issue—Bering Sea Seabird Synthesis.

Introduction

The southeastern Bering Sea is characterized by long- and short-term variability in oceanographic conditions. On a decadal scale the region as a whole exists in a warm or cold regime (Stabeno et al. 2012). On smaller temporal scales (1-3 years) it shifts between cold years, characterized by extensive sea ice and a late retreat, and warm years, characterized by low sea ice coverage and an early retreat (Stabeno et al. 2012). Fluctuations in annual sea ice extent and the timing of its retreat have been linked to the timing and duration of primary production (Liu et al. 2016). It has been proposed that these oscillating oceanographic conditions affect the distribution and availability of forage fish to marine predators, including seabirds (Hunt et al. 2011). This well-studied system provides a natural setting in which to address how sub-Arctic species may respond to future changes in the marine environment. We used it to examine how seabirds use and partition resources during a period when the southeastern Bering Sea shifted between very cold and very warm years (1999-2016, Overland et al. 2012, Stabeno et al. 2012).

Resource partitioning is considered to be an important mechanism by which species are able to reduce competition for common resources and co-exist (Schoener 1974, Finke & Snyder 2008). How food resources are partitioned in the ocean may be dynamic, driven by environmental factors affecting the availability of prey (e.g., Friedlaender et al. 2011, Sabarros et al. 2012). In seabirds, sympatrically breeding species are known to partition resources horizontally (Cherel et al. 2008, Rayner et al. 2016), vertically (Navarro et al. 2015, Kokubun et al. 2016), diurnally (Barger et al. 2016), and/or by prey type (Moreno et al. 2016, Rayner et al. 2016) or size (Mancini & Bugoni 2014). The degree of partitioning can depend upon changes in food availability (Barger & Kitaysky 2012), or can occur during energetically taxing life stages such as offspring provisioning (Cherel et al. 2008, Cherel et al. 2014, Barger et al. 2016, Delord et al. 2016).

Habitat heterogeneity may also affect resource partitioning. Access to different types of habitat may reduce interspecific competition for resources. For example, when foraging in a complex habitat, stone crabs (*Menippe mercernaria*) and knobbed whelks (*Busycon carica*) maintain consumption rates and feed upon similar prey species because the two predators are able to forage in different types of habitat (Hughes & Grabowski 2006). How access to diverse foraging habitats may modify interspecific resource partitioning under different environmental conditions in seabirds is, however, not well known. To better understand this issue we examined food resource partitioning among seabirds across multiple years in relation to changing oceanographic conditions and habitat heterogeneity.

Seabirds in the southeastern Bering Sea have access to different types of habitat depending on where they breed (Fig. 3.1). St. Paul Island is a relatively small colony located on the continental shelf. In contrast, St. George Island is a large colony that affords seabirds access to shelf, slope, and basin foraging habitats. These two islands are located 60 km apart (Byrd et al. 2008a). Tracking studies have revealed

that murres and kittiwakes rarely forage in the area between the two colonies, and that there is little overlap in their shelf and slope foraging locations (Harding et al. 2013, Paredes et al. 2014).

Using blood samples collected over the past 16 years we examined the isotopic niche dynamics of three piscivorous seabird species breeding on the Pribilof Islands to determine whether and how oceanographic conditions and habitat heterogeneity affected interspecific resource partitioning. The foraging behavior of seabirds is known to change throughout the course of the breeding season in response to the demands of their offspring (Navarro et al. 2014, Barger et al. 2016) as well as changes in prey resources (Scioscia et al. 2014, Jakubas et al. 2016). We analyzed red blood cells and plasma (with relatively slow and fast turn-over rates, see Methods) separately to characterize the arrival (early) and chick-rearing (late) periods of the breeding season to capture seasonal prey-use dynamics.

Hobson and colleagues (e.g., Hobson et al. 1994) showed that stable isotope analysis can be used to determine the trophic-level and general foraging habitat (inshore vs. offshore) used by 22 different seabird species. Stable isotope analysis has also proven to be a useful, non-invasive tool to reconstruct adult seabird diets (e.g. Silva-Costa & Bugoni 2013), identify shifts in diet (e.g. Cherel et al. 2014, Kowalcyzk et al. 2015), and determine how sympatric species partition prey resources (e.g. Young et al. 2010, Barger & Kitaysky 2012, Jaeger et al. 2014). Stable isotope ratios capitalize on the differential rate that heavy and light non-decaying isotopes of elements are used in biological processes. By analyzing samples for carbon and nitrogen isotopic ratios we can construct a predator's isotopic niche (Bearhop et al. 2004, Newsome et al. 2007), which describes where (reflected in carbon, $\delta^{13}C$) and at what trophic level (reflected in nitrogen, $\delta^{15}N$) it has been foraging. Isotopic niches have proven useful in discerning ecological segregation of marine species (e.g., tuna Ménard et al. 2007, dolphins Gross et al. 2009, myctophids Cherel et al. 2010), mapping food webs (e.g., Linnebjerg et al. 2016), and inferring food web diversity (e.g., Yurkowski et al. 2016).

We included three seabird species (which we refer to as a "group", Fig. 3.1) that use different parts of the horizontal and vertical foraging space. Black-legged kittiwakes ("kittiwakes") are able to travel comparatively far from the breeding colony, yet as surface feeders they have limited access to deeper layers of the water column. Common (*Uria aalge*) and thick-billed murres (*U. lomvia*) are relatively restricted in the distance they can travel from the colony, but are pursuit-diving foragers and have access to prey throughout the entire water column (up to 200 m in depth). Common murres, compared to thick-billed murres, are able to fly greater distances, and the two partition their use of the water column by time of day, distance from the breeding colony, and by foraging depth (Barger et al. 2016, Kokubun et al. 2016).

Previous work has found that in cold years, murres and kittiwakes breeding on the Pribilof Islands incurred relatively high levels of nutritional stress, suggesting that food was scarce or difficult to obtain

(Paredes et al. 2012, Satterthwaite et al. 2012). In warm years, however, they had relatively low levels of nutritional stress, indicating that food was abundant or more easily obtained (Benowitz-Fredericks et al. 2008, Satterthwaite et al. 2012, Harding et al. 2013, Paredes et al. 2014). When conditions are warm, primary production on the southeastern Bering Sea shelf supports large cohorts of young-of-the-year walleye pollock (*Gadus chalcogramma*) (Hunt et al. 2011), which can make up a large portion of murre and kittiwake diets (Renner et al. 2012, Sinclair et al. 2008). Thus, we predicted that the isotopic niche of seabirds would vary between cold and warm conditions in response to changes in prey availability.

In the southeastern Bering Sea there is a $\delta^{13}C$ gradient: prey on the continental shelf have an enriched carbon stable isotope signature compared to prey on the continental slope or ocean basin (Zeppelin et al. 2015), which is also reflected in the stable isotope signatures of bird blood tissues (Dorresteijn et al. 2012). In cold conditions, when juvenile pollock are scarce on the shelf, we predicted that the isotopic niche of birds with access only to homogenous foraging habitat (St. Paul) would expand as species separated themselves in space. In cold years St. Paul kittiwakes have been observed to forage near the continental slope (Paredes et al. 2014) whereas murres, which are unable to fly as far, continue to forage on the shelf near the breeding colonies (Harding et al. 2013). In contrast, we predicted that the isotopic niche used by seabirds on colonies closer to the shelf break would contract (more similar stable isotope signatures) during cold years. On St. George all species have access to more heterogeneous foraging habitat, so we would expect seabirds to concentrate their foraging efforts on prey inhabiting the continental slope region, there being low prey availability on the shelf (Pomerleau et al. 2014, Zeppelin et al. 2015, Suryan et al. 2016).

Methods

Study Sites and Sample Collection

Murres and kittiwakes were captured using noose poles on St. Paul (57.18119ºN, 170.266ºW) and St. George (56.580507ºN, 169.605925ºW) Islands between 1 July and 25 August (see Table 3.1 for years and sample sizes). No more than 1 ml of blood was collected from the alar vein and stored on ice (for details of capture and sampling see Benowitz-Fredericks et al. 2008). Within 12 hours of collection, blood was separated via centrifugation into plasma and red blood cells, and stored frozen until further analysis.

Stable Isotope Analysis

We used the isotopic composition of red blood cells and plasma to characterize seabird diets for the duration of the breeding season. Red blood cells reflect the dietary experience of birds about 2 months prior to the sampling date, thus our red blood cell samples captured the diets of birds arriving at the

colony and initiating their clutches ("arrival" Hobson & Clark 1993). Plasma turns over more quickly and reflects an individual's diet in the prior week (5-7 days Hobson & Clark 1993).

Red blood cells have a C:N ratio resembling pure protein (about 3.5, Cherel et al. 2014), therefore no preparation prior to analysis was needed. We freeze-dried a 20 µl sub-sample of red blood cells and loaded 0.1 – 0.6 mg into a tin boat for analysis. Plasma samples have a relatively high lipid content, which depletes the carbon signature and may lead to spurious results (Hobson & Clark 1992, Post et al. 2007). We delipidated a 20 µl sub-sample of plasma using a 1:4 methanol:choloroform solution (as described in Barger et al. 2016). Post-delipidation we freeze-dried samples and loaded 0.1 – 0.6 mg into a tin boat for analysis. For delipidated samples where C:N ratios remained high (>4, Cherel et al. 2005) we used the equation for aquatic organisms in Post et al. (2007) to subsequently quantitatively correct for carbon depletion ($\Delta^{13}C = -3.32 + 0.99 \cdot$ C:N, where $\Delta^{13}C$ is the correction factor applied to the $\delta^{13}C$ values).

Samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility (UAF SIF). Tin boats were loaded into an Elemental Analyzer (EA Costech ESC 4010) and processed via continuous flow isotope ratio mass spectrometry using a Delta+XP isotope ratio mass spectrometer. Ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ were calibrated using an internal standard (peptone: replicate measures indicated measurement errors of ± 0.34 ‰ and ± 0.08 ‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively) and then compared to the international standard ratios of atmospheric nitrogen and Vienna Pee Dee Belemnite using $\delta X = [(R_{sample}/R_{standard})-1]$ ‰, where X = ^{15}N or ^{13}C. Results are expressed in delta notation as parts per thousand (Peterson & Fry 1987).

Statistical Analysis

We conducted all statistical analysis in R (v. 3.2.3, R Core Development Team 2015). To determine whether years in our study had "warm" or "cold" oceanographic conditions we used principal components analysis (*prcomp* package, R Core Development Team 2015) to assign a continuous value to each year based on measurements from five climate indices. We included the summer Pacific Decadal Oscillation index (PDOs, averaged for June, July and August, http://www.beringclimate.noaa.gov/data/) which captures the variability in sea surface temperature across the North Pacific; the ice cover index (ICI, http://www.beringclimate.noaa.gov/data), the average ice concentration January to May reported as anomalies against the long-term mean; the ice retreat index (IRI, http://www.beringclimate.noaa.gov/data, the number of days after March 15 when > 10% of ice disappears from near buoy M2); and the sea surface and bottom temperature within a 150 km radius of the Pribilof Islands (Lauth 2016). These variables were selected to capture large and small scale variability and have been shown to be biologically

relevant (seabirds: Dorresteijn et al. 2012, Satterthwaite et al. 2012; zooplankton and fish: Stabeno et al. 2012).

Prior to examining isotopic niche dynamics we modeled carbon and nitrogen as a function of oceanographic conditions, colony, species, and season. The purpose for this was two-fold: 1) to verify that changes in oceanographic conditions correlated to changes in $\delta^{15}N$ or $\delta^{13}C$ values, and 2) to determine how to build the models to best describe the isotopic niche dynamics in the region. If, for example, all species on both colonies responded the same during both the arrival and chick-rearing period to oceanographic changes, then we would model the isotopic niches in a single model, not differentiating between colony or time during the breeding season. On the other hand, if two-way interactions indicated that species responded differently on different islands then we would model the isotopic niche using two models, one for each island. We used a random intercept mixed model (*lme4* package, Bates et al. 2015) and maximum likelihood estimation to separately model carbon and nitrogen with respect to the two islands (fixed effect: Colony), species (fixed effect: Species), time of the breeding season (fixed effect: Season), and oceanographic conditions (warm vs. cold) as modeled with the first principal components score (fixed effect: PC1). Although plasma and red blood samples were obtained from the same individuals, we included individual as a random factor. We included the two-way and three-way interactions of these variables to determine whether species from different colonies behaved similarly (indicated by non-significant interaction terms) under different oceanographic conditions and/or across a season. We used Akaike's Information Criteria (AICc for small sample sizes) to select the best candidate model, which we used to determine how to structure our analysis of the isotopic niche dynamics (Burnham & Anderson 2002).

We used the R package *SIBER* (Jackson et al. 2011) to analyze the stable isotope data at the foraging group and species level. We used a Bayesian approach to calculate Layman metrics, a set of summary statistics that describe changes in the shape, size, and concentration of points within the isotopic ellipse (Layman et al. 2007), for our focal seabird group and to calculate the standard ellipse area for each individual species under different oceanographic conditions. We categorized years as "warm" or "cold" according to our principal components analysis (described above) and included them in the model as the "community" variable (i.e. all warm and all cold years were combined). We ran a Markov-chain Monte Carlo with 2 chains drawing from a Wishart distribution, with vague normal priors, for 20,000 iterations, and a burn in of 1,000. Every 10^{th} value of the posterior was retained (Jackson et al. 2011). Following Jackson et al. (2011) the Layman metrics we report include the standard ellipse area (SEA), dX_range (dC), dY_range (dN), which give the range of the group along the X (carbon) and Y (nitrogen) axis, total area of the group (TotArea), distance to the centroid (Centroid), average distance to a point's nearest neighbor (NNdist), and the standard deviation of the nearest neighbor distance (sdNNdist). We calculated

the mode and credible intervals for the standard ellipse areas of each species under warm and cold conditions. Finally, means and standard errors for carbon and nitrogen values of each species were calculated based on the raw data to capture shifts in the isotopic niche at the species level.

Results

Principal Components Analysis of Climate Variables

PC1 retained 91.34% of the variance in the component variables. All five components were loaded for PC1 (PDO = 0.906, ICI = -0.982, IRI = -0.98, Bottom = 0.951, SST = 0.957), and contributed a similar amount to determining the score (PDO = 17.968, ICI = 21.135, IRI = 21.019, Bottom = 19.803, SST = 20.075). The designation of "warm" and "cold" years based on PC1 corresponded to characterizations of the study years in the literature (Fig. 3.2, Stabeno et al. 2012).

Mixed Model Results

Carbon stable isotope ratios were best described by two models (Table 3.2). One model (AICweight = 0.529) included PC1, Species, Colony, and Season as fixed effects, two-way interactions between Season*Species, Season*Colony, and Species*Colony, and a three-way interaction among Season*Species*Colony. The other best candidate model (AICweight = 0.468), included all four fixed effects and PC1 (in place of Season) in the two-way and three-way interaction terms (PC1*Species, PC1*Colony, Species*Colony, and PC1*Species*Colony).

Both models suggested that PC1 was a significant predictor of carbon signatures, as PC1 increased (conditions warm), carbon signatures become more enriched (Model 1 $t_{343} = 14.53$, $p < 0.0001$; Model 2 $t_{343} = -2.53$, $p = 0.0117$). Both models indicated that St. Paul birds had significantly more enriched carbon signatures than birds on St. George ($t_{343} = 5.77$, and $t_{343} = 10.48$, $p < 0.0001$ for both models). According to the first model, carbon stable isotope ratios changed differently on the two different colonies among species (Species*Colony: t_{343}, $p < 0.001$), and species on the two islands responded differently over the course of the breeding season (Season*Species*Colony: $t_{343} = 4.58$, $p < 0.001$). In this model the differing responses of species was largely driven by changes in common murre stable isotope signatures within the breeding season (Season*Species: $t_{343} = -2.55$, $p = 0.011$). According to the second model, the carbon stable isotope ratios among the species were different under different oceanographic conditions (PC1*Species: $F_{343} = 31.1$, $p < 0.0001$) and at the two colonies (a Species*Colony: $F_{343} = 19.7$, $p < 0.0001$). Carbon stable isotope ratios on the two colonies in general responded differently to oceanographic conditions (PC1*Colony: $F_{343} = 5.1$, $p < 0.0001$), and the inter-species patterns of the response was also different (PC1*Species*Colony: $F_{343} = 9.7$, $p < 0.0001$).

Nitrogen stable isotope ratios were best described by a model including PC1, Species, Colony, and Season as fixed effects as well as a three-way interaction between PC1*Season*Species, and the two-way interactions therein (PC1*Season, PC1*Species, Season*Species; Table 3.3). This model had an AIC weight of 0.763 compared to the next best model with a weight of 0.226, which included all of the same terms except for the three-way interaction.

Nitrogen stable isotope ratios were significantly different between colonies ($F_{343} = 345.76$, $p < 0.0001$) and among species ($F_{343} = 31.27$, $p < 0.0001$), and tended to be depleted early in the season (red blood cells: $t_{343} = 1.97$, $p < 0.049$). The direction that nitrogen signatures changed within the breeding season and among species was different in warm compared to cold conditions (PC1*Season: $F_{343} = 27.32$, $p < 0.0001$; PC1*Species: $F_{343} = 15.65$, $p < 0.0001$). Nitrogen signatures among species changed in different directions within a breeding season (Species*Season: $F_{343} = 17.9$, $p < 0.0001$), which was somewhat influenced by oceanographic conditions (Species*Season*PC1: $F_{343} = 3.22$, $p = 0.041$).

Group Analysis

Based on our mixed model results we calculated Layman metrics for the seabird group on St. Paul and St. George under warm and cold conditions respectively. dC provides a description of trophic diversity and dN characterizes the breadth of the food web's base. "TotArea" represents an estimate of the total diversity encompassed by a group's niche. "Centroid" is a measure of the average diversity used in the food web. "NNdist" complements Centroid by reporting the distribution of species within the total area, with a small NNdist indicating that species are foraging in a similar isotopic space. sdNNdist characterizes the evenness of the distribution of isotopic niches within a group, with low sdNNdist values indicating even spacing of species within the total area.

The isotopic niche of breeding seabirds on St. George expanded during warm conditions (Fig. 3.2). This expansion was most pronounced early in the breeding season as illustrated by significant differences in the group parameters for red blood cells. During warm conditions trophic level diversity increased (dN), as did the overall diversity of the utilized food web (Centroid), and the degree of species packing (NNdist, Fig. 3.3A). The total area covered by our three study species increased somewhat in warm conditions (Fig. 3.4). The isotopic niche during chick-rearing (characterized by plasma stable isotope signatures) responded similarly, expanding somewhat in area during warm conditions (TotArea, Fig. 3.4). Increased variability in the plasma signatures, however, resulted in overlapping credible intervals for all five measures, making it difficult to discern any clear responses at the group level to warmer conditions during the chick-rearing period.

Birds on St. Paul had the opposite response to warmer conditions (Fig. 3.3C and D). Birds tended to forage in a smaller geographic range during arrival (dC, Fig. 3.3C), but otherwise responses to early

oceanographic conditions were not pronounced. Later in the season (during chick-rearing) the isotopic niche contracted during warm conditions (Fig. 3.3D). This contraction was characterized by a significant decrease in the diversity of trophic levels utilized (dN), and a tendency to decrease the geographic diversity of their foraging area (dC, Fig.3.3D). Most notably trophic diversity decreased during warm conditions (Centroid) and the trophic niche of individual species tended to converge (NNdist, Fig. 3.3D). In general, during warm conditions birds on St. Paul utilized a less diverse and smaller isotopic niche than birds on St. George.

Species Ellipses

On St. George all species in all conditions expanded the area of their isotopic niche as the breeding season progressed (Fig. 3.3A and B). The standard ellipse area of black-legged kittiwakes during arrival did not change between cold and warm conditions, and only moderately decreased in warm conditions during chick-rearing (Fig. 3.5). In contrast to kittiwakes, both murre species responded to changes in early season conditions. The area of common murres' isotopic niche expanded (Fig. 3.5), and shifted to more on-shelf and higher trophic level food sources (Fig. 3.6). The area of thick-billed murres' isotopic niche contracted, and did not shift in location (Fig. 3.5). Common murres maintained a seasonal pattern of niche expansion in cold compared to warm years, focused primarily along the $\delta^{13}C$ (geographic) axis (Fig. 3.5, Fig. 3.6). Conversely, during chick-rearing thick-billed murres showed no difference in their isotopic niche area between cold and warm conditions (Fig. 3.5), but did shift their niche towards on-shelf resources and higher trophic level prey in warm conditions (Fig. 3.6).

The isotopic niche dynamics of birds breeding on St. Paul indicate that responses to oceanographic conditions were different among the three species (Fig. 3.5). The isotopic niche of surface-feeding black-legged kittiwakes expanded in cold compared to warm conditions, but remained consistent throughout the breeding season (Fig. 3.5). The area of common murres' isotopic niche expanded over the course of the breeding season during cold conditions, but remained the same when conditions were warm (Fig. 3.4). Thick-billed murres expanded their isotopic niche in cold compared to warm conditions both in the early and late stages of the breeding season (Fig. 3.5). All three species consumed more shelf-based prey during warm conditions (Fig. 3.6).

Discussion

Prey distribution and composition in the southeastern Bering Sea change in response to climate conditions and may affect the foraging behavior and diets of breeding seabirds. Efforts to detect relationships in this region between diet composition of omnivorous seabirds and regional climate indices have, however, failed to find any consistent trends (Renner et al. 2012, Renner et al. 2014). In contrast,

patterns in habitat use have been documented regularly (Schneider & Hunt 1982, Hunt et al. 2014, Renner et al. 2016, Suryan et al. 2016). The diets of murres and black-legged kittiwakes have been documented to be diverse, including forage fish and invertebrate species (Renner et al. 2012, Iverson et al. 2007, Sinclair 2008). Thus it may be that instead of focusing on particular prey species, these seabirds rely on oceanographic features such as eddies (Paredes et al. 2014), tidal fronts (Coyle et al. 1992, Ladd et al. 2005), and/or the thermocline (Takahashi et al. 2008) to guide their foraging efforts. Instead of manifesting changes in prey in response to environmental change, omnivorous seabirds in the Bering Sea may instead change the location and trophic level at which they feed.

To understand this, we characterized the isotopic niche of black-legged kittiwakes and murres breeding on St. Paul and St. George Islands in warm and cold years. Isotopic niches have proven useful in determining the way in which sympatrically breeding seabirds partition the foraging habitat by geographic location and trophic level (e.g. Navarro et al. 2015, Cherel et al. 2007, Moreno et al. 2016). Previous work in the eastern Bering Sea has used this approach to examine resource partitioning among breeding common and thick-billed murres with access to a single habitat type. The isotopic distance between common and thick-billed murres increased during years when food was limited (Barger & Kitaysky 2012), and during the energetically taxing chick-rearing period in a year when food was abundant (Barger et al. 2016). It may be expected that species engaging in similar foraging modes would partition prey when interspecific competition is more likely to occur (during food shortages or chick-rearing). Whether or not species using the same habitat but with a dissimilar foraging strategy will also modify their foraging niche during food shortages had not been examined. Thus, it was not clear whether characterizing the niche of a diverse group of seabirds would be an informative method to detect changes in the marine food web. In this study we investigated how food resources were partitioned among three seabird species under different oceanographic conditions and with access to different habitat types. We predicted that all species would modify their foraging niche in response to food shortages and that access to multiple habitat types would reverse the niche dynamics of seabirds during food abundant and food-poor years.

Seabirds breeding on both St. Paul and St. George shifted to consuming more shelf-based prey under warm oceanographic conditions. This may have been a response to an increased abundance of juvenile pollock on the shelf in warm years (Suryan et al. 2016, Renner et al. 2016, Hunt et al. 2011). In warm years juvenile pollock have been observed closer to the ocean surface and occur at 51 times the densities recorded in cold years (Renner et al. 2016). At-sea surveys indicated that surface-feeding black-legged kittiwakes and moderately deep-diving shearwaters (*Ardenna* spp.) occurred in greater abundance over the shelf region in warm years with early ice retreat (Renner et al. 2016). Whether a greater abundance of pollock is also beneficial for murres has been unclear, as water masses and prey at depth

may be somewhat independent of the dynamics shaping the food web available to surface foragers (Byrd et al. 2008b, Renner et al. 2016). Our results, however, indicate that common murres, and to some extent thick-billed murres, shifted towards shelf-based prey on St. George and St. Paul, suggesting that they may also be feeding on pollock in warm years. Despite this signal that all three species on both colonies in some way took advantage of more abundant shelf-based prey in warm years, we found that isotopic niche dynamics on the two colonies were different both seasonally and between warm and cold years.

Seasonal Isotopic Niche Dynamics

In cold conditions the trophic diversity used by our focal group on St. Paul significantly increased (i.e., isotopic niche expansion) over the course of the breeding season, the result perhaps of an additive effect of poor foraging conditions and an increase in energy demands associated with chick-rearing (Barger et al. 2016). In warm years on St. Paul, on-shelf prey appeared to be abundant; kittiwakes and common murres maintained their narrow isotopic niche throughout the breeding season. In contrast, thick-billed murres on St. Paul and all three species of birds on St. George displayed an expansion in the isotopic niche during chick-rearing irrespective of oceanographic conditions. This indicates that intraspecific diet diversification during chick-rearing may have occurred and may have been due to seasonal changes in prey type and/or availability (Darimont & Reimchen 2002), allowing individual specialization to occur (Newsome et al. 2009).

On St. George in warm years, access to diverse habitat and to on-shelf young-of-the-year pollock "subsidies" may facilitate prey specialization by individuals in all years regardless of oceanographic conditions (Darimont et al. 2009). During warm conditions on St. George, the isotopic niche of murres and kittiwakes expanded in all aspects compared to cold conditions, indicating that while birds used on-shelf prey, it did not replace the use of oceanic-based prey. Early in the breeding season in warm years, the isotopic niche of seabirds increased both in geographic and trophic diversity, indicating that both shelf and oceanic-based prey were consumed. Black-legged kittiwakes and common murres accounted for most of the shelf-based prey use early in the season. As the season progressed, the use of shelf-based prey dwindled for kittiwakes and common murres, but increased somewhat for thick-billed murres.

Isotopic Niche Dynamics of the Seabird Group with Respect to Habitat

The isotopic niche of the St. Paul seabird group was heavily influenced by ocean conditions. In warm years it contracted in all aspects during arrival and chick-rearing with one exception: prior to breeding the diversity in foraging locations was comparable to cold conditions, as reflected in the dN and dC isotopic distances. This may be a signal that the food web on the shelf developed from a common starting point early in the breeding season, but that the trajectory of development may have been

determined by oceanographic conditions that resulted in an increasingly different foraging landscape as the season progressed (Hunt et al. 2011).

In warm years the isotopic space used by seabirds on St. George (closer to the shelf break) was significantly more diverse and larger than the isotopic space used by seabirds on St. Paul (farther from the shelf break), whereas in cold years the total areas used at the two islands were similar. This may be partially attributed to the differences in colony size between the two islands. St. George supports an order of magnitude more seabirds than St. Paul (Hickey & Craighead 1977), indicating that access to the shelf and slope foraging habitats potentially allows more individuals to meet their energetic needs during the breeding season (Ashmole 1963, Furness & Birkhead 1984). It may, however, also encourage the maintenance of slope foraging habitat during warm years when shelf food resources are abundant. The isotopic niche dynamics suggest that omnivorous seabirds breeding on St. George used oceanic-based prey, both during warm conditions when alternative shelf-based prey was available, and especially in cold conditions when it was not. The analysis of stomach contents collected from adult birds corroborate our finding that the slope/oceanic region provides an important prey-base for St. George seabirds (Sinclair et al. 2008, Renner et al. 2012, Harding et al. 2013). Fledging success of thick-billed murres on both islands has been positively correlated to the occurrence of coastal/shelf-based species in chick diets, which Renner and colleagues (e.g., Renner et al. 2014) suggest is due to the energetic savings parents make by being able to capture prey closer to the colony (Elliott et al. 2013, Pennycuick 1997).

Closing Remarks

To summarize, we found that during warm years omnivorous seabirds had access to and consumed prey on the shelf that was not available to them during cold years. In addition, species with access to multiple habitat types were able to exploit the appearance of new prey sources, but continued to use prey in all available habitats. We found that food resource partitioning increased over the course of the breeding season regardless of oceanographic conditions, potentially indicative of seasonal changes in prey diversity, and/or increased individual specialization during a period of increased energy demand. Our results suggest that warm conditions are currently beneficial for murres and black-legged kittiwakes breeding on the Pribilof Islands. Whether this would remain the case under prolonged periods of warming remains to be seen. Warm conditions in late summer and autumn result in low recruitment of young-of-the-year pollock (Hunt et al. 2011, Mueter et al. 2011), thus, an increase in the frequency of warm years may eventually result in a negative impact on seabirds through reduced pollock populations (Mueter et al. 2011). According to our results, a decline in pollock would have the greatest impact on birds breeding on St. Paul Island.

More generally we demonstrated that the isotopic niche can be used to characterize how seabirds, with different foraging strategies, partition the foraging landscape in response to food shortages. In omnivorous seabird species that may have access to diverse prey, we showed that the isotopic niche can be an informative tool to detect responses to changes in prey availability, which may not be observable through the noise inherent in commonly employed methods of estimating diet composition. In this study we specifically addressed whether or not having access to diverse foraging habitat may modify how seabirds partition resources under different oceanographic conditions. We found that knowledge of habitat type, and how prey dynamics in different habitats may change, is needed in order to correctly interpret the expansion or contraction of the isotopic niche used by a group of species as a response to changes in prey availability. In regards to the southeastern Bering Sea specifically, we conclude that the isotopic niche of omnivorous seabirds breeding on the Pribilof Islands responded to changes in oceanographic conditions, and showed that the manifestation of this response was mediated by habitat heterogeneity.

Acknowledgements

This work could not have been completed without the collection, preparation, or analysis of samples as part of other research over the past 16 years. We would like to thank (alphabetically) Yumi Arumitzu, Allison Banks, Chris Barger, Morgan Benowitz-Fredericks, Tom Dempsey, Ine Dorresteijn, Brie Drummond, Abram Fleishman, Motohiro Ito, Sara Iverson, Dale Kikuchi, Zhenya Kitaiskaia, Nobuo Kokubun, Rachael Orben, John Piatt, Nobuhiro Sato, Michael Shultz, Alan Springer, Akinori Takahashi, Shiway Wang, Takashi Yamamoto, Rebecca Young, and Sarah Youngren. Stable isotope analysis of plasma samples for this study was funded by a Calvin J Lensink Fellowship awarded to A.Will and was completed by Tim Howe and Norma Haubenstock at the Alaska Stable Isotope Facility (Thank You!). Red blood cell stable isotope analysis was conducted as part of the North Pacific Research Board's (NPRB) Bering Sea Integrated Ecosystem Research Project #67 and 77 awarded to A. Kitaysky. Input from G. Breed, A. Powell, and A. Springer greatly improved this manuscript. All samples were collected under the required permits from the U.S. Fish and Wildlife Service and Alaska Department of Fish and Game with the approval of the University of Alaska Fairbanks' Institutional Animal Care and Use Committee.

References

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. Ibis 103b: 458-473

Barger CP, Kitaysky AS (2012) Isotopic segregation between sympatric seabird species increases with nutritional stress. Biology Letters 8:442-445

Barger CP, Young RC, Will A, Ito M, Kitaysky AS (2016) Resource partitioning between sympatric seabird species increases during chick- rearing. Ecosphere 7:e01447

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007-1012

Benowitz-Fredericks ZM, Shultz MT, Kitaysky AS (2008) Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. Deep-Sea Research Part II: Topical Studies in Oceanography 55:1868-1876

Burnham KP, Anderson DR (2002) Model selection and multimodal inference: a practical information-theoretic approach. Springer-Verlag, New York

Byrd GV, Schmutz JA, Renner HM (2008a) Contrasting population trends of piscivorous seabirds in the Pribilof Islands: A 30-year perspective. Deep-Sea Research II 55:1846–1855

Byrd GV, Sydeman WJ, Renner HM, Minobe S (2008b) Responses of piscivorous seabirds at the Pribilof Islands to ocean climate. Deep-Sea Research II 55:1856–1867

Cherel Y, Connan M, Jaeger A, Richard P (2014) Seabird year-round and historical feeding ecology: blood and feather $\delta^{13}C$ and $\delta^{15}N$ values document foraging plasticity of small sympatric petrels. Marine Ecology Progress Series 505:267-280

Cherel Y, Corre ML, Jaquemet S, Ménard F, Richard P, Weimerskirch H (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. Marine Ecology Progress Series 366:281-291

Cherel Y, Fontaine C, Richard P, Labatc J-P (2010) Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. Limnology and Oceanography 55:324-332

Cherel Y, Hobson KA, Guinet C, Vanpe C (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. Journal of Animal Ecology 76:826-836

Cherel Y, Hobson KA, Weimerskirch H (2005) Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. Oecologia 145:533–540

Coyle KO, Hunt Jr. GL, Decker MB, Weingartner TJ (1992) Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. Marine Ecology Progress Series 83:1-14

Darimont CT, Paquet PC, Reimchen TE (2009) Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. Journal of Animal Ecology 78:126-133

Darimont CT, Reimchen TE (2002) Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. Canadian Journal of Zoology 80:1638-1642

Delord K, Pinet P, Pinaud D, Barbaud C, de Grissac S, Lewden A, Cherel Y, Weimerskirch H (2016) Species-specific foraging strategies and segregation mechanisms of sympatric Antarctic fulmarine petrels throughout the annual cycle. IBIS 158:569–586

Dorresteijn I, Kitaysky AS, Barger C, Benowitz-Fredericks ZM, Byrd GV, Shultz M, Young R (2012) Climate affects food availability to planktivorous least auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea. Marine Ecology Progress Series 454:207-220

Elliott KH, Ricklefs RE, Gaston AJ, Hatch SA, Speakman JR, Davoren GK (2013) High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. PNAS 110: 9380-9384

Finke DL, Snyder WE (2008) Niche partitioning increases resource exploitation by diverse communities. Science 321:1488-1489

Friedlaender AS, Johnston DW, Fraser WR, Burns J, Patrick N H, Costa DP (2011) Ecological niche modeling of sympatric krill predators around Marguerite Bay, western Antarctic Peninsula. Deep-Sea Research Part II: Topical Studies in Oceanography 58:1729-1740

Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311:655-656

Gross A, Kiszka J, Van Canneyt O, Richard P, Ridoux V (2009) A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, southwest Indian Ocean. Estuarine, Coastal and Shelf Science 84:367-374

Harding A, Paredes R, Suryan R, Roby D, Irons D, Orben R, Renner H, Young R, Barger C, Dorresteijn I, Kitaysky A (2013) Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. Deep-Sea Research Part II: Topical Studies in Oceanography 94:178-191

Hickey JJ, Craighead FL (1977) A census of seabirds on the Pribilof Islands. In: Environmental Assessment of the Alaskan Continental Shelf. Final Reports of Principal Investigators, BLM/NOAA/OMPA Boulder CO USA 2:96–195

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786-798

Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. The Condor 94:181-188

Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. The Auk 110:638-641

Hughes AR, Grabowski JH (2006) Habitat context influences predator interference interactions and the strength of resource partitioning. Oecologia 149:256-264

Hunt Jr. GL, Coyle KO, Eisner LB, Farley EV, Heintz RA, Mueter F, Napp JM, Overland JE, Ressler PH, Salo S, Stabeno PJ (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES Journal of Marine Science 68:1230-1243

Hunt Jr. GL, Renner M, Kuletz K (2014) Seasonal variation in the cross-shelf distribution of seabirds in the southeastern Bering Sea. Deep-Sea Research II 109:266-281

Hunt Jr. GL, Stabeno PJ, Strom S, Napp JM (2008) Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. Deep-Sea Research 55:1919-1944

Iverson SJ, Springer AM, Kitaysky AS (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analysis using fatty acids. Marine Ecology Progress Series 352:235-244

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER– Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602

Jaeger A, Goutte A, Lecomte VJ, Richard P, Chastel O, Barbraud C, Weimerskirch, Cherel Y (2014) Age, sex, and breeding status shape a complex foraging pattern in an extremely long-lived seabird. Ecology 95:2324-2333

Jakubas D, Wojczulanis-Jakubas K, Boehnke R, Kidawa D, Błachowiak-Samołyk K, Stempniewicz L (2016) Intra-seasonal variation in zooplankton availability, chick diet and breeding performance of a high Arctic planktivorous seabird. Polar Biology 39:1547-1561

Kokubun N, Yamamoto T, Sato N, Watanuki Y, Will A, Kitaysky AS, Takahashi A (2016) Foraging segregation of two congeneric diving seabird species breeding on St. George Island, Bering Sea. Biogeosciences: Discussions 13:2579–2591

Kowalczyk ND, Reina RD, Preston TJ, Chiaradia A (2015) Environmental variability drives shifts in the foraging behaviour and reproductive success of an inshore seabird. Oecologia 178:967-979

Ladd C, Jahncke J, Hunt Jr. GL, Coyle KO, Stabeno PJ (2005) Hydrographic features and seabird foraging in Aleutian Passes. Fisheries Oceanography 14:178-195

Lauth B (2016) Eastern Bering Sea Trawl Data. National Oceanic and Atmospheric Administration.

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42-48

Linnebjerg JF, Hobson KA, Fort J, Nielsen TG, Møller P, Wieland K, Born EW, Rigét FF, Mosbech A (2016) Deciphering the structure of the West Greenland marine food web using stable isotopes ($\delta^{13}C$, $\delta^{15}N$). Marine Biology 163:230

Liu CL, Zhai L, Zeemand SI, Eisner LB, Ganne JC, Mordy CW, Morang SB, Lomas MW (2016) Seasonal and geographic variations in modeled primary production and phytoplankton losses from the mixed layer between warm and cold years on the eastern Bering Sea shelf. Deep-Sea Research II 134:141-156

Mancini PL, Bugoni L (2014) Resource partitioning by seabirds and their relationship with other consumers at and around a small tropical archipelago. ICES Journal of Marine Science 71:2599-2607

Ménard F, Lorrain A, Potier M, Marsac F (2007) Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) of the western Indian Ocean. Marine Biology 153:141-152

Moreno R, Stowasser G, McGill RAR, Bearhop S, Phillips RA (2016) Assessing the structure and temporal dynamics of seabird communities: the challenge of capturing marine ecosystem complexity. Journal of Animal Ecology 85:199–212

Mueter FJ, Bond NA, Ianelli JN, Hollowed AB (2011) Expected declines in recruitment of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea under future climate change. ICES Journal of Marine Science 68:1284-1296

Navarro J, Cardador L, Brown R, Phillips RA (2015) Spatial distribution and ecological niches of non-breeding planktivorous petrels. Scientific Reports 5:12164

Navarro J, Moreno R, Braun L, Sanpera C, Hennicke JC (2014) Resource partitioning between incubating and chick-rearing brown boobies and red-tailed tropicbirds on Christmas Island. Zoological Studies 53:27

Newsome SD, Marinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429-436

Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90:961-974

Overland JE, Wang M, Wood KR, Percival DB, Bond NA (2012) Recent Bering Sea warm and cold events in a 95-year context. Deep-Sea Research II 65-70:6-13

Paredes R, Harding AMA, Irons DB, Roby DD, Suryan RM, Orben RA, Renner H, Young R, Kitaysky A (2012) Proximity to multiple foraging habitats enhances seabirds' resilience to local food shortages. Marine Ecology Progress Series 471:253-269

Paredes R, Orben RA, Suryan RM, Irons DB, Roby DD, Harding AMA, Young RC, Benoit-Bird K, Ladd C, Renner H, Heppell S, Phillips RA, Kitaysky A (2014) Foraging responses of black-legged kittiwakes to prolonged food shortages around colonies on the Bering Sea shelf. PloS ONE 9:e92520

Pennycuick CJ (1997) Actual and 'optimum' flight speeds: field data reassessed. The Journal of Experimental Biology 200:2355-2361

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320

Pomerleau C, Nelson RJ, Hunt BPV, Sastri AR, Williams W (2014) Spatial patterns in zooplankton communities and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) in relation to oceanographic conditions in the sub-Arctic Pacific and western Arctic regions during the summer of 2008. Journal of Plankton Research 36:757-775

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189

R Core Development Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing

Rayner MJ, Carlile N, Priddel D, Bretagnolle V, Miller MGR, Phillips RA, Ranjard L, Bury SJ, Torres LG (2016) Niche partitioning by three *Pterodroma* petrel species during non-breeding in the equatorial Pacific Ocean. Marine Ecology Progress Series 549:217-229

Renner HM, Drummond BA, Benson A-M, Paredes R (2014) Reproductive success of kittiwakes and murres in sequential stages of the nesting period: relationships with diet and oceanography. Deep-Sea Research II 109:251-265

Renner HM, Mueter F, Drummond BA, Warzybok JA, Sinclair EH (2012) Patterns of change in diets of two piscivorous seabird species during 35 years in the Pribilof Islands. Deep-Sea Research II 65-70:273–291

Renner M, Salo S, Eisner LB, Ressler PH, Ladd C, Kuletz KJ, Santora JA, Piatt JF, Drew GS, Hunt Jr. GL (2016) Timing of ice retreat alters seabird abundances and distributions in the southeast Bering Sea. Biology Letters 12: 20160279

Sabarros PS, Durant JM, Grémillet D, Crawford RJM, Stenseth NC (2012) Differential responses of three sympatric seabirds to spatio-temporal variability in shared resources. Marine Ecology Progress Series 468:291-301

Satterthwaite WH, Kitaysky AS, Mangel M (2012) Linking climate variability, productivity and stress to demography in a long-lived seabird. Marine Ecology Progress Series 454:221-235

Schneider D, Hunt Jr. GL (1982) A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska. In: Nettleship DN, Songer GA, Springer PF (eds.) Proceedings of the Pacific Seabird Group Symposium, Seattle WA Canadian Wildlife Service Special Publication.

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27-39

Scioscia G, Raya Rey A, Saenz Samaniego RA, Florentín O, Schiavini A (2014) Intra- and interannual variation in the diet of the Magellanic penguin (*Spheniscus magellanicus*) at Martillo Island, Beagle Channel. Polar Biology 37:1421-1433

Silva-Costa A, Bugoni L (2013) Feeding ecology of Kelp Gulls (*Larus dominicanus*) in marine and limnetic environments. Aquatic Ecology 47:211-224

Sinclair EH, Vlietstra LS, Johnson DS, Zeppelin TK, Byrd GV, Springer AM, Ream RR, Hunt Jr. GL (2008) Patterns in prey use among fur seals and seabirds in the Pribilof Islands. Deep-Sea Research II 55:1897-1918

Stabeno PJ, Kachel NB, Moorec SE, Napp JM, Sigler M, Yamaguchif A, Zerbini AN (2012) Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep-Sea Research II 65-70:31-45

Suryan RM, Kuletz KJ, Parker-Stetter SL, Ressler PH, Renner M, Horne JK, Farley EV, Labunski EA (2016) Temporal shifts in seabird populations and spatial coherence with prey in the southeastern Berin Sea. Marine Ecology Progress Series 549:199-215

Takahashi A, Matsumoto K, Hunt Jr. GL, Shultz MT, Kitaysky AS, Sato K, Iida K, Watanuki Y (2008) Thick-billed murres use different diving behaviors in mixed and stratified waters. Deep-Sea Research II 55:1837-1845

Young HS, McCauley DJ, Dirzo R, Dunbar RB, Shaffer SA (2010) Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. Marine Ecology Progress Series. 416:285-294

Yurkowski DJ, Ferguson S, Choy ES, Loseto LL, Brown TM, Muir DC, Semeniuk CA, Fisk AT (2016) Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. Ecoligy and Evolution 6:1666-1678

Zeppelin TK, Johnson DS, Kuhn CE, Iverson SJ, Ream RR (2015) Stable isotope models predict foraging habitat of northern fur seals (*Callorhinus ursinus*) in Alaska. PloS ONE 10: e0127615

Figures

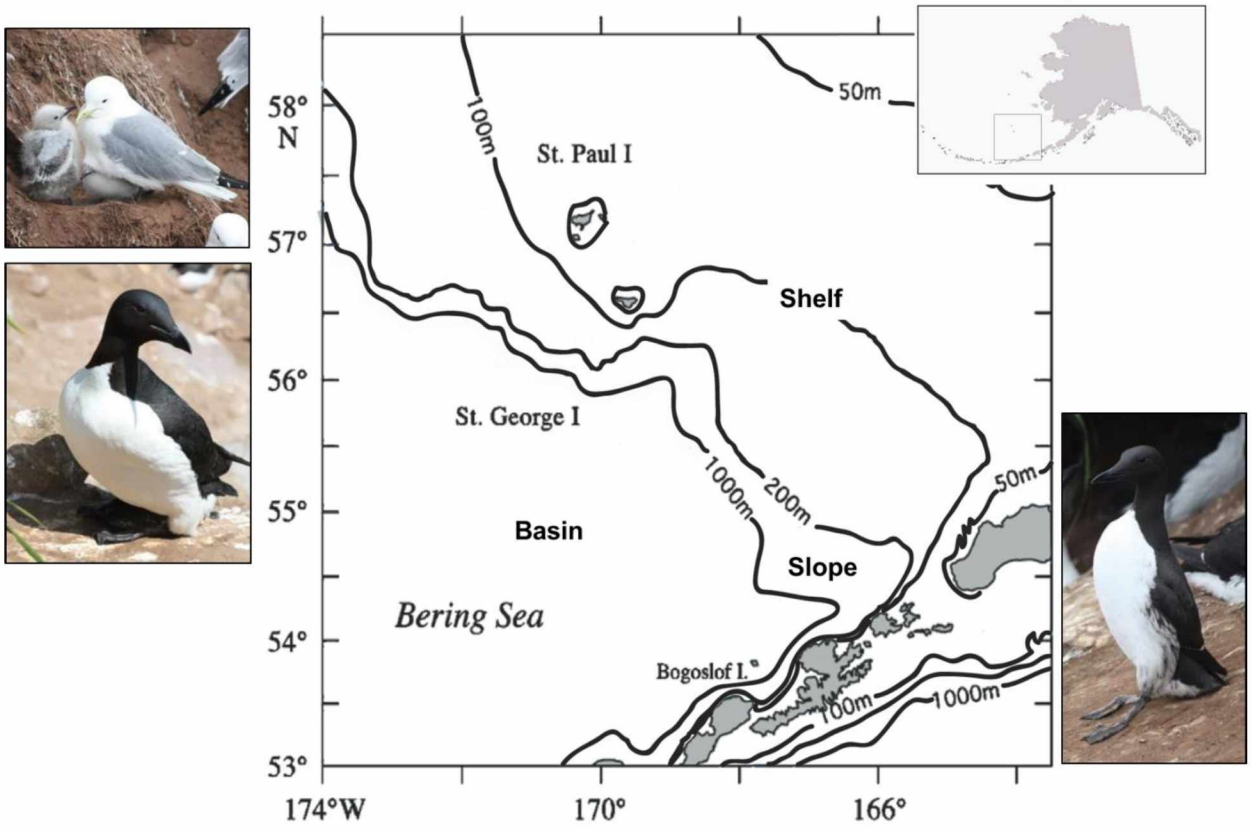

Figure 3.1 Study area and focal species. St. Paul and St. George Islands are located on the continental shelf, 90 and 25 km from the shelf-break respectively. Pictured clockwise from top to bottom are a black-legged kittiwake with chick, a common murre, and a thick-billed murre (photo credit: A. Will, map adapted from Hunt et al. 2008).

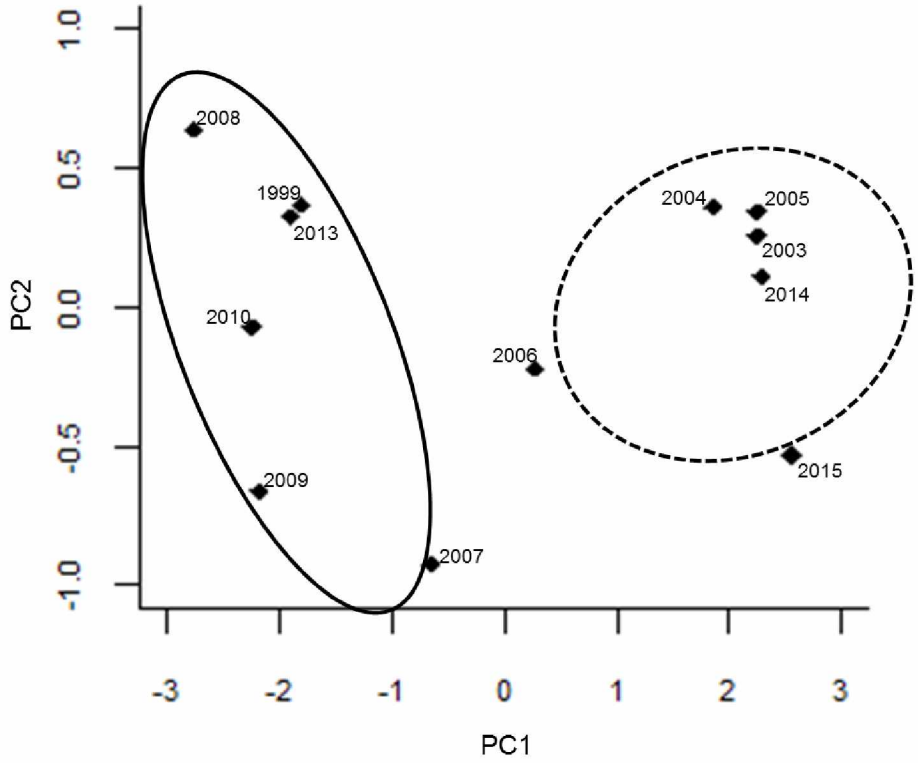

Figure 3.2 Using PC1 we categorized years as being "cold" or "warm". Negative numbers corresponded to cold oceanographic conditions and positive numbers corresponded to warm oceanographic conditions. PC1 is plotted against PC2. The ellipses indicate the cold (solid line) and warm (dashed line) groupings. The year corresponding to each point is noted within the plot.

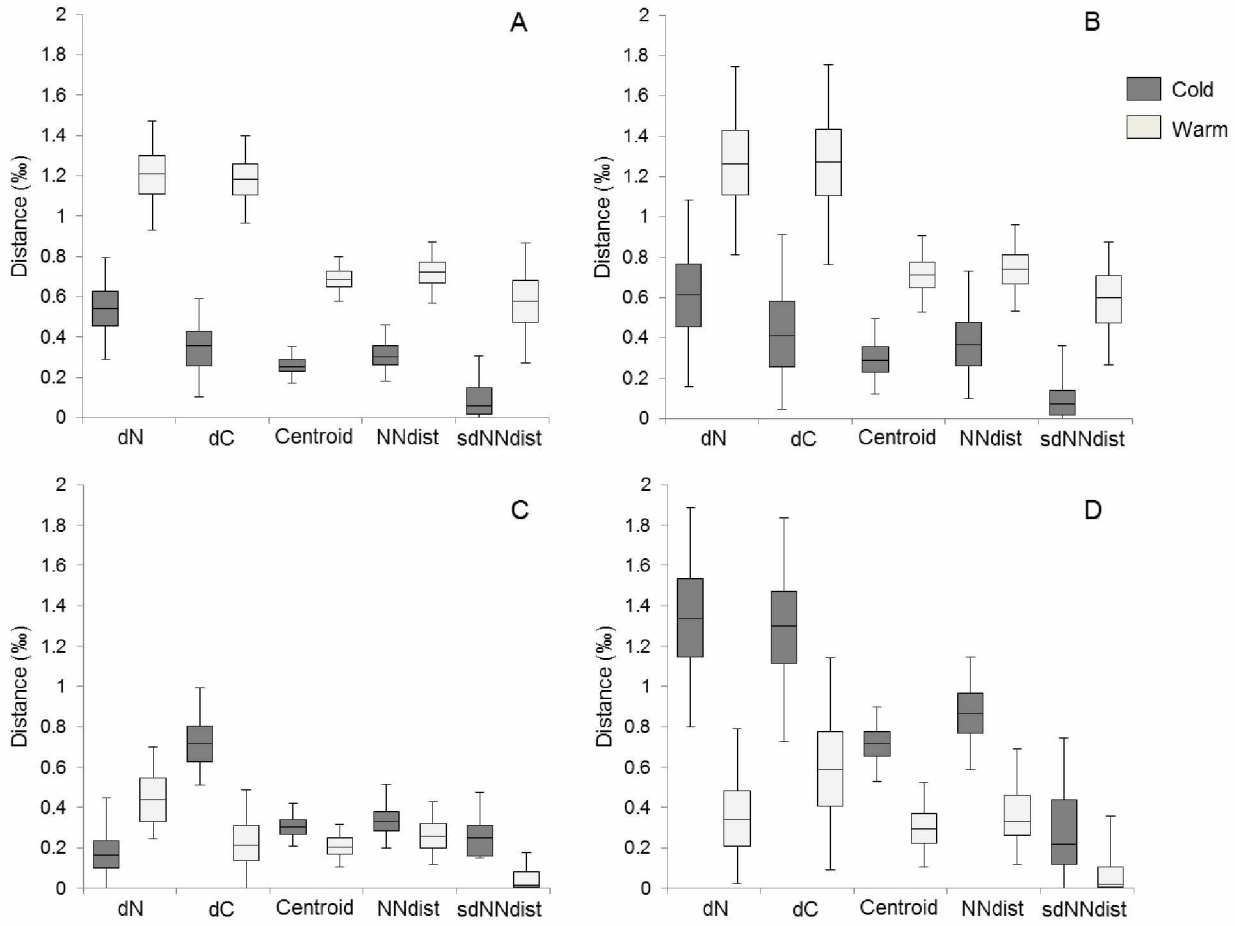

Figure 3.3 During warm years the seabird group expanded its isotopic niche on St. George (A, B) and contracted it on St. Paul (C, D) Islands. Laymen metrics calculated for the seabird group are posterior modes, 50% (box) and 90% (whisker) credible intervals are of the seabird group displayed for cold (dark grey) and warm (light grey) conditions. Panels illustrate changes between cold and warm conditions on (A) St. George Island during arrival, (B) St. George Island during chick-rearing, (C) St. Paul Island during arrival, and (D) St. Paul Island during chick-rearing. See Methods for a description of parameters.

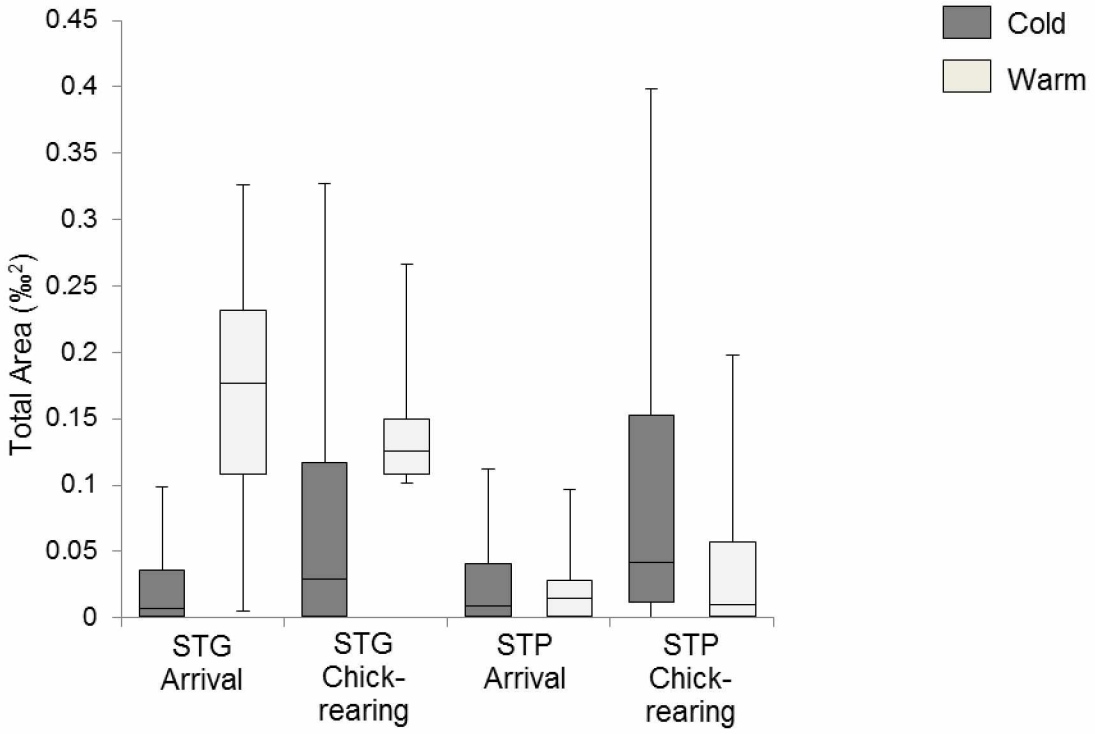

Figure 3.4 On St. George Island the total area of the seabird group's isotopic niche increased in warm years. This increase occurred during both the arrival and chick-rearing period. St. Paul showed little difference in the total area used by all three species in warm or cold years. Dark grey indicates cold conditions, light grey indicates warm conditions. Displayed are the mode, and the 50% (box) and 99% (whiskers) credible intervals.

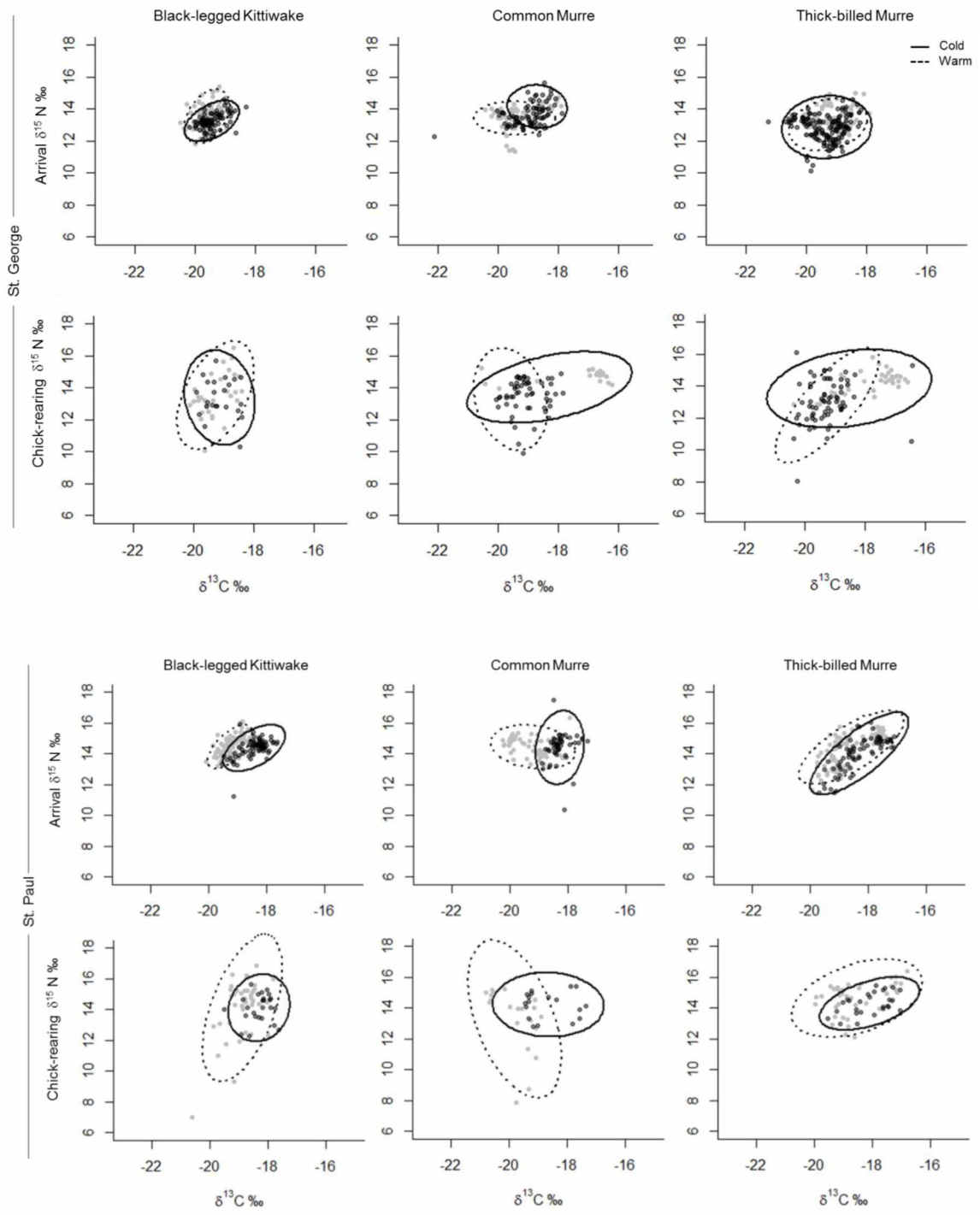

Figure 3.5 At the species level, isotopic niches on St. Paul contracted and those on St. George expanded during warm oceanographic conditions. Displayed are stable isotope signatures of red blood cells ("Arrival") and plasma ("Chick-rearing") for black-legged kittiwakes and murres breeding on St. George and St. Paul Islands in cold (black) and warm (grey) conditions. Super-imposed are the standard ellipse areas for each species during cold (solid line) and warm (dashed line) conditions.

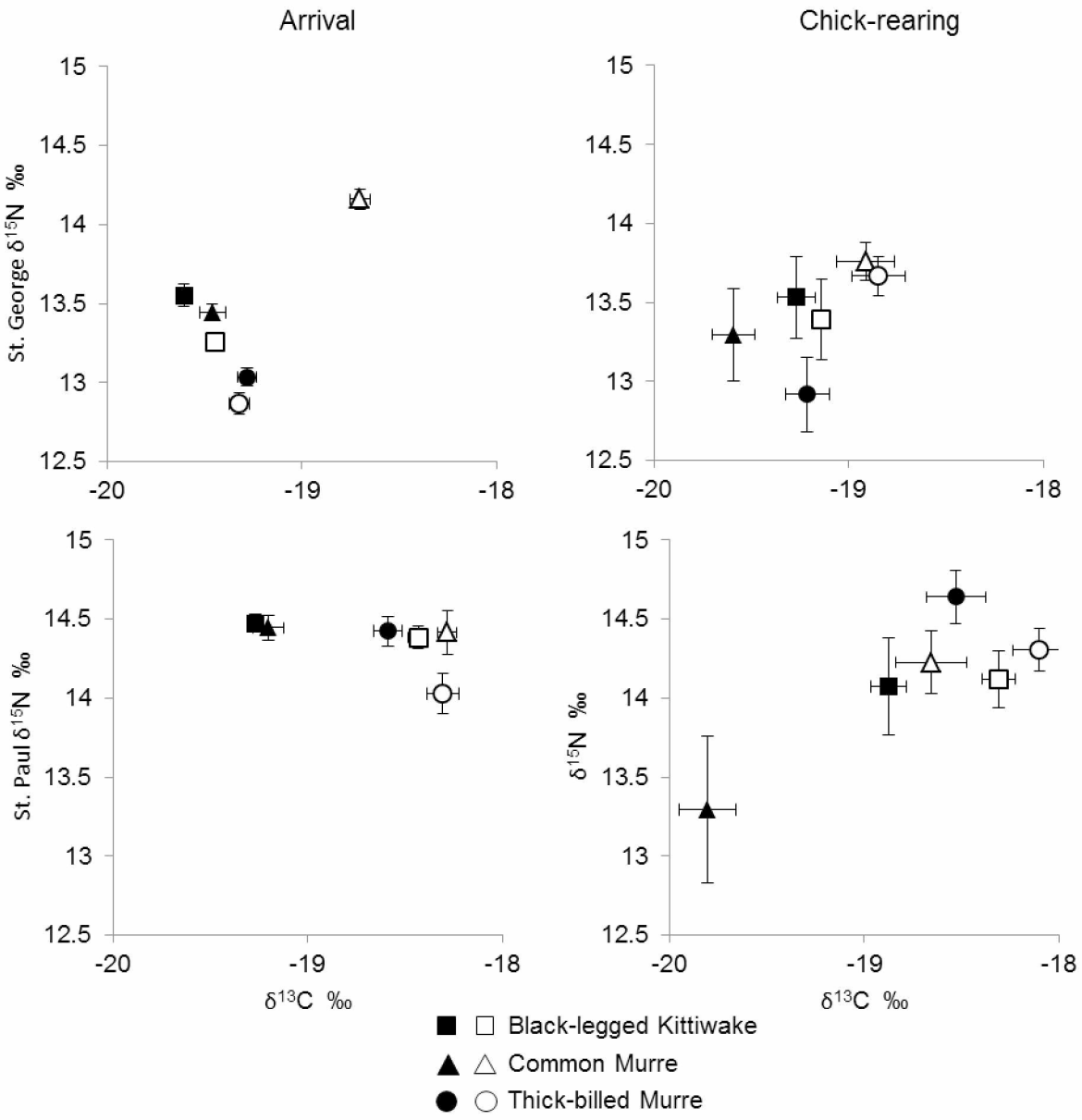

Figure 3.6 The average stable isotope values for species breeding on St. George (top panel) and St. Paul (bottom panel) Islands. Mean (± SE) isotopic signatures of black-legged kittiwakes, and murres shifted between cold and warm oceanographic conditions (within figures) and between the arrival (first column) and chick-rearing (second column) periods of the breeding season.

Tables

Table 3.1 Sample sizes by island, year, and tissue. All except 2015 plasma values are from individuals whose red blood cells were also analyzed. BLKI = black-legged kittiwake, COMU = common murre, TBMU = thick-billed murre.

	Red Blood Cells				Plasma		
Island	**BLKI**	**COMU**	**TBMU**	**Year**	**BLKI**	**COMU**	**TBMU**
St. George	-	10	10	**1999**	-	-	-
St. Paul	10	-	10		9	-	7
St. George	30	21	30	**2003**	8	8	9
St. Paul	30	18	30		10	8	10
St. George	28	26	30	**2004**	8	10	10
St. Paul	31	24	25		10	8	10
St. George	26	18	29	**2005**	7	9	9
St. Paul	15	8	18		5	2	7
St. George	-	-	22	**2006**	-	-	-
St. Paul	-	-	-		-	-	-
St. George	-	-	32	**2007**	-	-	-
St. Paul	-	-	-		-	-	-
St. George	31	22	27	**2008**	10	10	10
St. Paul	30	28	30		10	10	10
St. George	26	37	28	**2009**	9	10	10
St. Paul	24	26	30		10	10	10
St. George	36	-	33	**2010**	10	-	9
St. Paul	35	-	39		10	-	10
St. George	-	-	-	**2013**	-	-	30
St. Paul	-	-	-		-	-	-
St. George	-	14	38	**2014**	-	14	18
St. Paul	-	-	-		-	-	-
St. George	-	-	-	**2015**	-	15	20
St. Paul	-	-	-		-	-	-
St. George	177	148	279	**Totals**	52	76	125
St. Paul	175	104	182		64	38	64

Table 3.2 AIC model selection results for carbon. We report the top six models, as well as the single variable and additive model. All other models had an AIC weight of 0. "Sps" = species, "Col" = colony, "Seas" = season. We tested 47 models. All models include bird as a random effect. A full list of the candidate models is reported in the Appendix.

all with bird as random effect	***k***	**AICc**	**ΔAICc**	w_i
*PC1+Sps+Col+Seas+Seas*Sps+Seas*Col+Sps*Col+Seas*Sps*Col*	*9*	*2741.19*	*0.00*	*0.529*
*PC1+Sps+Col+Seas+PC1*Sps+PC1*Col+Sps*Col+PC1*Sps*Col*	*9*	*2741.43*	*0.24*	*0.468*
PC1+Sps+Col+Seas+PC1*Seas+PC1*Sps+Seas*Sps+PC1*Seas*Sps	9	2752.23	11.04	0.002
PC1+Sps+Col+PC1*Sps+PC1*Col+Sps*Col+PC1*Sps*Col	8	2754.95	13.76	0.000
PC1+Sps+Col+Seas+PC1*Sps+Seas*Col	7	2776.87	35.69	0.000
PC1+Sps+Col+Seas+Seas*Col+PC1*Sps	7	2776.87	35.69	0.000
PC1+Sps+Col+Seas	5	2847.35	106.16	0.000
PC1	2	3066.69	325.50	0.000
Sps	2	3166.39	425.20	0.000
Col	2	3086.98	345.79	0.000
Seas	2	3185.66	444.47	0.000
null model	2	3193.26	452.07	0.000

Table 3.3 AIC model selection results for nitrogen. We report the top six models, as well as the single variable and additive model. All other models had an AIC weight of 0. "Sps" = species, "Col" = colony, "Seas" = season. We tested 49 models. All models include bird as a random effect. A full list of the candidate models is reported in the Appendix.

all with bird as random effect	***k***	**AICc**	**ΔAICc**	w_i
*PC1+Sps+Col+Seas+PC1*Seas+PC1*Sps+Seas*Sps+PC1*Seas*Sps*	*9*	*3981.87*	*0.00*	*0.763*
PC1+Sps+Col+Seas+PC1*Seas+PC1*Sps+Seas*Sps	8	3984.31	2.43	0.226
PC1+Sps+Col+Seas+Seas*Sps+Sps*Col+Seas*Col+Seas*Sps*Col	9	3991.47	9.59	0.006
Sps+Col+Seas+Seas*Sps+Col*Sps+Seas*Col	7	3993.84	11.97	0.002
Sps+Col+Seas+Seas*Sps+Sps*Col+Seas*Col+Seas*Sps*Col	8	3994.50	12.63	0.001
PC1+Sps+Col+PC1*Sps+PC1*Col+Sps*Col+PC1*Sps*Col	8	3995.04	13.17	0.001
PC1+Sps+Col+Seas	5	4066.10	84.23	0.000
PC1	2	4392.06	410.18	0.000
Sps	2	4347.62	365.75	0.000
Col	2	4108.96	127.08	0.000
Seas	2	4391.70	409.83	0.000
null model	2	4390.14	408.26	0.000

Appendix 3.A: Complete List of Candidate Models

Table 3.A-1 Candidate models for carbon stable isotope signatures. Best fit models are highlighted in grey.

Models, all with Individual as random effect	k	AICc	ΔAICc	w_i
null model	2	3193.260	452.070	0.000
PC1+Species+Colony+Season	5	2847.349	106.160	0.000
PC1	2	3066.692	325.502	0.000
Species	2	3166.386	425.196	0.000
Colony	2	3086.984	345.794	0.000
Season	2	3185.658	444.468	0.000
PC1+Species	3	3043.436	302.246	0.000
PC1+Colony	3	2907.209	166.019	0.000
PC1+Season	3	3055.934	314.744	0.000
Species+Colony	3	3040.209	299.019	0.000
Species+Season	3	3161.270	420.080	0.000
Colony+Season	3	3075.567	334.377	0.000
PC1+Species+Colony+Season+PC1*Species	6	2794.035	52.845	0.000
PC1+Species+Colony+Season+PC1*Colony	6	2844.960	103.770	0.000
PC1+Species+Colony+Season+PC1*Season	6	2843.568	102.378	0.000
PC1+Species+Colony+Season+Species*Season	6	2829.326	88.136	0.000
PC1+Species+Colony+Season+Species*Colony	6	2804.423	63.233	0.000
PC1+Species+Colony+Season+Colony*Season	6	2827.748	86.558	0.000
PC1+Species+Colony+PC1*Species	5	2806.257	65.068	0.000
PC1+Species+Season+PC1*Species	5	2996.010	254.821	0.000
PC1+Species+PC1*Species	4	3003.088	261.898	0.000
PC1+Species+Colony+PC1*Colony	5	2858.437	117.248	0.000
PC1+Season+Colony+PC1*Colony	5	2889.096	147.907	0.000
PC1+Colony+PC1*Colony	4	2906.058	164.868	0.000
PC1+Season+Colony+PC1*Season	5	2887.076	145.887	0.000
PC1+Season+Species+PC1*Season	5	3036.170	294.981	0.000
PC1+Season+PC1*Season	4	3056.619	315.429	0.000
Species+Season+Colony+Species*Season	5	3019.477	278.288	0.000
PC1+Species+Season+Species*Season	5	3012.583	271.394	0.000
Species+Season+Species*Season	4	3144.088	402.898	0.000
Species+Colony+Season+Species*Colony	5	2992.429	251.240	0.000
PC1+Species+Colony+Species*Colony	5	2818.818	77.629	0.000
Species+Colony+Species*Colony	4	3001.337	260.147	0.000
PC1+Season+Colony+Colony*Season	5	2890.390	149.201	0.000
Species+Season+Colony+Season*Colony	5	3031.670	290.481	0.000
Season+Colony+Season*Colony	4	3075.582	334.392	0.000
PC1+Species+Season+Colony+PC1*Species+Season*Colony	7	2776.875	35.685	0.000
PC1+Species+Season+Colony+PC1*Colony+Season*Species	7	2827.492	86.302	0.000
PC1+Species+Season+Colony+Season*Colony+PC1*Species	7	2776.875	35.685	0.000
PC1+Season+Colony+Species+PC1*Season*Colony	9	2813.279	72.089	0.000
PC1+Season+Colony+PC1*Season*Colony	8	2856.257	115.067	0.000
PC1+Species+Colony+Season+PC1*Species*Colony	9	2741.433	0.243	0.468
PC1+Species+Colony+PC1*Species*Colony	8	2754.954	13.764	0.001
PC1+Season+Species+Colony+Season*Species*Colony	9	2741.190	0.000	0.529
Season+Species+Colony+Season*Species*Colony	8	2935.910	194.720	0.000
PC1+Season+Species+Colony+PC1*Season*Species	9	2752.231	11.041	0.002
PC1+Season+Species+PC1*Season*Species	8	2960.756	219.566	0.000

Table 3.A-2 Candidate models for nitrogen stable isotope signatures. Best fit models are highlighted in grey.

Models, all with Individual as random effect	k	AICc	ΔAICc	w_i
null model	2	4390.138	408.265	0.000
PC1+Species+Colony+Season	5	4066.100	84.228	0.000
PC1	2	4392.058	410.185	0.000
Species	2	4347.623	365.750	0.000
Colony	2	4108.957	127.084	0.000
Season	2	4391.705	409.832	0.000
PC1+Species	3	4349.575	367.702	0.000
PC1+Colony	3	4105.239	123.366	0.000
PC1+Season	3	4393.621	411.748	0.000
Species+Colony	3	4067.135	85.262	0.000
Species+Season	3	4349.400	367.527	0.000
Colony+Season	3	4110.815	128.942	0.000
PC1+Species+Colony+Season+PC1*Species	6	4037.698	55.825	0.000
PC1+Species+Colony+Season+PC1*Colony	6	4056.063	74.190	0.000
PC1+Species+Colony+Season+PC1*Season	6	4042.187	60.314	0.000
PC1+Species+Colony+Season+Species*Season	6	4041.296	59.423	0.000
PC1+Species+Colony+Season+Species*Colony	6	4031.915	50.042	0.000
PC1+Species+Colony+Season+Colony*Season	6	4050.965	69.092	0.000
PC1+Species+Colony+PC1*Species	5	4035.686	53.814	0.000
PC1+Species+Season+PC1*Species	5	4334.156	352.284	0.000
PC1+Species+PC1*Species	4	4332.626	350.753	0.000
PC1+Species+Colony+PC1*Colony	5	4054.110	72.238	0.000
PC1+Season+Colony+PC1*Colony	5	4097.674	115.802	0.000
PC1+Colony+PC1*Colony	4	4095.707	113.834	0.000
PC1+Season+Colony+PC1*Season	5	4081.645	99.773	0.000
PC1+Season+Species+PC1*Season	5	4337.246	355.374	0.000
PC1+Season+PC1*Season	4	4378.929	397.056	0.000
Species+Season+Colony+Species*Season	5	4044.746	62.874	0.000
Species+Season+PC1+Species*Season	5	4331.856	349.984	0.000
Species+Season+Species*Season	4	4329.996	348.123	0.000
Species+Colony+Season+Species*Colony	5	4034.891	53.019	0.000
Species+Colony+PC1+Species*Colony	5	4030.070	48.198	0.000
Species+Colony+Species*Colony	4	4033.098	51.225	0.000
PC1+Season+Colony+Colony*Season	5	4092.693	110.821	0.000
Species+Season+Colony+Season*Colony	5	4053.433	71.561	0.000
Season+Colony+Season*Colony	4	4095.882	114.009	0.000
PC1+Species+Season+Colony+PC1*Species+Season*Colony	7	4024.484	42.611	0.000
PC1+Species+Season+Colony+PC1*Colony+Season*Species	7	4029.510	47.637	0.000
PC1+Species+Season+Colony+Season*Colony+PC1*Species	7	4024.484	42.611	0.000
PC1+Season+Colony+Species+PC1*Season*Colony	9	4024.447	42.574	0.000
PC1+Season+Colony+PC1*Season*Colony	8	4064.568	82.695	0.000
PC1+Species+Colony+Season+PC1*Species*Colony	9	3997.069	15.196	0.000
PC1+Species+Colony+PC1*Species*Colony	8	3995.045	13.172	0.001
PC1+Species+Season+Colony+PC1+Season*Species*Colony	9	3991.468	9.595	0.006
Species+Season+Colony+Season*Species*Colony	8	3994.500	12.627	0.001
PC1+Species+Season+Colony+PC1*Season*Species	9	3981.873	0.000	0.763
PC1+Species+Season+PC1*Season*Species	8	4295.559	313.686	0.000
Species+Season+Colony+Season*Species+Colony*Species+Season*Colony	7	3993.840	11.967	0.002
PC1+Species+Season+Colony+PC1*Season+PC1*Species+Season*Species	8	3984.307	2.434	0.226

Chapter 4 Red-legged Kittiwake Feathers Link Food Availability to Environmental Changes in the Bering Sea Basin Over a 100 Year Period[6].

Abstract

The world's largest breeding population of the red-legged kittiwake (*Rissa brevirostris*), which relies almost exclusively on the Bering Sea basin for prey, underwent a dramatic decline and subsequent recovery in the past four decades. The causal mechanism for the period of decline has been hypothesized to have been stress incurred by birds as a result of climate-induced food shortages during reproduction. Yet little is known about how the basin ecosystem is affected by climate variability, and it is unclear under what conditions prey in the Bering Sea basin become unavailable to red-legged kittiwakes and whether these food shortages may have extended into the wintering stage of the birds' annual cycle. We employed a historical ecophysiology approach to examine when and under what conditions red-legged kittiwakes historically experienced food shortages. We collected head feathers (grown during the end of the wintering period) and first primary feathers (grown during the breeding season) from St. George Island, the species' principle breeding location, from 1913 to the present (n = 24 and 27 years; and 194 and 122 individuals, respectively). We analyzed feathers for stable-isotope signatures of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to characterize birds' foraging niche, and for corticosterone which is passively deposited in feathers during molt and indicates a bird's exposure to nutritional stress. We found that both summer and winter feather corticosterone (fCORT) was lower when values of the annual Pacific Decadal Oscillation Index (PDO) were positive. Winter fCORT concentrations and $\delta^{15}N$ signatures increased when February sea ice coverage was extensive, suggesting birds may lose access to preferred foraging habitat and may experience higher stress during cold winters. Birds also incurred higher levels of winter stress during the period of population decline (1976-1989) compared to the period of population increase (1992-2014), indicating changes in environmental conditions were not limited to the reproductive season. We conclude that since 1913 warm conditions in the Bering Sea ecosystem have been associated with a reduction in nutritional stress incurred by adult red-legged kittiwakes breeding on St. George Island. However, we found no strong evidence for dietary shifts over this same period. A better understanding of the factors governing the abundance and availability of red-legged kittiwakes' prey is still needed in order to fully predict the impact of anticipated warming on this species and its foraging habitats.

[6] Will, Alexis; Kitaiskaia, Evgenia; Kitaysky, Alexander. In preparation for Marine Ecology Progress Series.

Introduction

The Bering Sea climate has historically oscillated between "warm" and "cold" states, characterized by changes in winter sea ice dynamics and storminess, and summer water temperatures (Rodionov & Overland 2005, Zhang et al. 2010). These changes in climate have been associated with fluctuations in the region's animal populations and community structure (Hare & Mantua 2000, Benson & Trites 2002, Aydina & Mueter 2007, Litzow & Mueter 2014). In the southeastern Bering Sea, population declines observed in seabird, marine mammal, and fish populations (Hare and Mantua 2000, Benson & Trites 2002, Litzow & Mueter 2014) during the late 1970s and 1980s are hypothesized to be a result of changes in food availability (Anonymous 1993). How food availability changed, however, is not certain.

One hypothesis posits that a coinciding explosion in the walleye pollock (*Gadus chalcogrammus*) population resulted in increased competition with other top predators for forage fishes (Springer 1992). Another proposes that oceanographic conditions were no longer suitable for lipid-rich forage fish species, and fish lower in lipid content, such as the now abundant juvenile pollock, were inadequate to meet the energy demands of predatory fish, seabirds, and marine mammal populations (Alverson 1992, the "junk-food hypothesis", also see Hunt et al. 1996, reviewed in Österblom et al. 2008). One other possible, not yet tested, explanation is that food shortages occurred during the winter, and affected animals outside of the reproductive season (e.g., during migration/overwinter, Renner et al. 2014).

In terms of seabird responses to climate-driven food availability, a great deal of work has been done to understand how climate-associated changes in the southeastern Bering Sea continental shelf ecosystem affect prey abundance (e.g., Napp et al. 2000, Hunt et al. 2002 and references therein, Springer et al. 2007, Hunt et al. 2011 and references therein) and seabird reproduction (e.g., Springer 1998, Byrd et al. 2008a, Byrd et al. 2008b, Zador et al. 2013, Renner et al. 2014, Springer & van Vliet 2014, Murphy et al. 2016). How or whether these same climate patterns affect forage fish production in the ocean basin, however, is less clear. Of the seabirds breeding in the southeastern Bering Sea, red-legged kittiwakes are the only fish-eating seabird that relies primarily on oceanic prey (Byrd and Williams 1993). Red-legged kittiwakes forage almost exclusively on myctophids, a mesopelagic fish, during the reproductive season (Storer 1987, Byrd and Williams 1993, Iverson et al. 2007, Kokubun et al. 2015). Thus, red-legged kittiwakes might be somewhat independent of the food dynamics of the southeastern Bering Sea continental shelf region, which govern the diets of other seabirds breeding on the Pribilof Islands (Jahncke et al. 2008, Renner et al. 2012, Renner et al. 2016). Furthermore the breeding population on St. George Island has shown dramatic changes in population trajectory over the past four decades (Byrd et al. 2008a), suggesting that the birds are experiencing changes in prey availability at some point in their annual cycle. Thus red-legged kittiwakes may provide insight into how this part of the Bering Sea ecosystem may have responded to past environmental variability. There is some evidence that red-legged

kittiwake reproductive success may be attributed to environmental conditions (Springer 1998), but a connection between environmental variability and food availability has yet to be made.

Research has shown that, for seabirds, changes in the environment can result in food shortages that are reflected in seabird physiology (e.g., Kitaysky et al. 1999, Satterthwaite et al. 2012). Nutritional stress incurred during reproduction affects adult seabird survival (Kitaysky et al. 2007, Kitaysky et al. 2010, Satterthwaite et al. 2010) and poor quality food fed to developing offspring may produce low-quality individuals that may be unable to recruit into the population (Kitaysky et al. 2006).

As a step towards resolving the relationship between changes in environmental conditions and the responses of red-legged kittiwakes, we used a historical ecophysiology approach to examine the diet and physiological response of St. George red-legged kittiwakes to environmental variability from 1913 to the present. Historical ecophysiology uses analytical tools to mine ecologically relevant measures from specimens or samples collected in the past, allowing researchers to greatly extend time series and rely on unified laboratory methodologies.

Red-legged kittiwakes undergo two annual molts. Towards the end of the breeding season (~July-August) adults initiate their flight feather molt, a sequential molt that begins with the loss of their first primary (Byrd & Williams 1993). In approximately February adults undergo a pre-nuptial molt where they replace, at a minimum, their non-breeding head feather plumage (Byrd & Williams 1993, Orben et al. 2015). To characterize conditions during the breeding (summer) and non-breeding (winter) periods, we collected first primary and head feathers from museum specimens and free-living individuals. We analyzed first primary ("primary") and head feathers for nitrogen and carbon stable isotope ratios. Stable isotopes are non-degrading versions of elements that have more neutrons than protons, and occur at known proportions in nature. Based on differential isotopic incorporation rates it is possible to identify trophic level (nitrogen, Fry 1988) and location (carbon, Hobson et al. 1994) of an organism in a marine food web based on the ratio of heavy (rare) to light (common) isotopes in their tissues (Peterson and Fry 1987, Hobson and Welch 1992). Thus, the combination of the annual molt and stable isotope signatures yields a proxy for summertime diet from first primaries and winter diet from head feathers.

While stable isotope analysis can be used to identify when diet changes occur, it does not fully capture how seabirds may be affected by changes in the environment. A change in conditions may be detrimental to seabirds but may not be accompanied by a shift in prey (e.g., Will et al. 2015 and references therein). For example, prey species may not change but may become more dispersed or less available and require more energy to obtain. Alternatively, birds may shift their diet among equally good prey types, so that a change in diet may not necessarily be detrimental.

Thus, to better understand the effect of variability in climate and diet on red-legged kittiwakes we also analyzed head and primary feathers for corticosterone concentration (Bortolotti et al. 2008).

Corticosterone is the avian stress hormone which, in kittiwakes, is indicative of nutritional stress (Kitaysky et al. 2006, Kitaysky et al. 2010). During molt, circulating corticosterone is deposited into the growing feather and provides an integrated measure of the nutritional stress a bird experienced during the period of feather growth. Elevated concentrations in feather corticosterone have been experimentally linked to low food intake (Will et al. 2014), validated as a proxy for low food availability (Will et al. 2014, Will et al. 2015) and are stable through time (Bortolotti et al. 2009). We analyzed feather corticosterone (fCORT) concentrations in the same feathers we used in the stable isotope analysis, characterizing the nutritional status of birds during the winter (~Feb.) and summer (~July, Byrd & Williams 1993). To determine how diet and nutritional stress change in response to changes in oceanographic conditions, we modeled nitrogen and carbon stable isotope ratios and fCORT concentrations in head and primary feathers as response variables to environmental parameters. We also specifically examined patterns in nutritional stress and population counts to determine whether winter conditions may have contributed to the population decline of the late 1970s and 1980s.

Methods

Study Site and Specimen Origin

All samples were collected from adult red-legged kittiwakes breeding on St. George Island, one of the Pribilof Islands, in the southeastern Bering Sea (56.58°N, 169.60°W). We sampled live birds and specimens from the following museums: Carnegie Museum of Natural History, Natural History Museum of Los Angeles County, Museum of Southwestern Biology, James R. Slater Museum, San Diego Natural History Museum, and University of Alaska Fairbanks' Museum of the North. Please refer to the Appendix for a complete list of specimens used in this study.

Feather Sampling

To minimize the impact of our study on museum collections we used only a small portion of a primary feather for our analyses, and whenever possible left the feather still attached to the museum skin. Specifically, we cut a 20 mm section, approx. 20 mm from the tip of the first primary along the proximal side of the vane. In the field, birds were captured using a noose pole, the first primary was clipped off at the base, and the same 20 mm section described above was later removed in the lab. For both museum and wild-caught birds we plucked 3 head feathers between the upper nape and crown of the head (see Appendix for samples by year).

Corticosterone Analysis

We weighed and measured (head feathers only) feathers to the nearest 0.05 mg and 0.5 mm. We combined all 3 head feathers (measuring each separately but weighing them collectively) into a single sample for each individual (Lattin et al. 2011). We washed feather samples in isopropanol (HPLC-grade, Sigma-Aldrich, St. Louis, MO): i.e., we added 1 ml of isopropanol to a vial containing the feather sample, vortexed for 5 seconds, and removed the isopropanol 50 seconds later. After the washing, we added 5 ml of methanol (HPLC-grade, Fisher Scientific, Waltham, MA) to each sample and proceeded with extraction and analysis procedures reported elsewhere (see Bortolotti et al. 2008, Will et al. 2015). We added 2,000 cpm of radio-labeled corticosterone (PerkinElmer NET399, Boston, MA) to each sample to account for losses of hormone during analysis. On average recoveries were 94.8%.

Feathers were analyzed in 5 separate radioimmunoassays (Wingfield & Farner 1975). Intra-assay CV was <1 % (range: 0.72 to 0.97 %) and inter-assay CV was 1.2 %. We standardized concentrations to sample mass (ng/g, primary feathers) and feather length (pg/mm, head feathers only).

Stable Isotope Analysis

After the methanol extraction, in the corticosterone analysis described above, feather samples were used for stable isotope analysis. We weighed out between 0.6 and 1 mg of pulverized primary feather tissues, or a single intact head feather, and loaded the sample material into a tin boat. Stable isotope analysis was conducted at the Alaska Stable Isotope Facility (ASIF, Fairbanks AK). Briefly, samples were loaded into an auto-sampler which dropped them into an elemental analyzer (EA Costech ECS 4010) interfaced with a Delta+XP Thermo Electron isotope ratio mass spectrometer. We used delta notation to express stable isotope ratios, "R", in comparison to Pee Dee Belamnite (carbon) and atmospheric nitrogen ($\delta X = R_{sample} / R_{standard}$). Peptone was used as an internal standard. We completed the analysis in 4 separate runs. Inter-run standards were within ± 0.01‰ for both $\delta^{15}N$ and $\delta^{13}C$ and on average intra-run standards were within ± 0.1‰ for both $\delta^{15}N$ and $\delta^{13}C$. Head feathers from 2010 and 2011 were analyzed by Orben et al. (2015) at the University of California Santa Cruz (UCSC); UCSC internal standards were comparable when run at ASIF (Appendix).

Environmental Variables

To detect course-grained patterns in the responses of red-legged kittiwake diet and physiology to long-term environmental variability we used regional climate indices that have been shown to be ecologically relevant and/or detect regime shifts. Environmental predictors for head feathers (fCORT and stable isotope signatures) were selected based on two criteria: 1) ecological relevance, and 2) a correlation of less than 0.5 with any other variable for the years included in our study. April sea ice coverage is the

one exception, we retained it in our models due to the potential ecological impacts on the return migration to the colony despite a high correlation (-0.76) with the annual Pacific Decadal Oscillation index (PDO, Mantua et al. 1997, Mantua and Hare 2002). Variables included in models of head feather parameters included: Year, PDO, the Arctic Oscillation (AO), and the February sea ice coverage (IceFeb), and for primary feathers: Year, PDO, the AO, the Aleutian Low (ALow), and the April sea ice coverage (IceApr).

We included Year in the model selection process to account for any trends over time not fully captured by the other parameters (Bond et al. 2003). In the case of carbon, Year accounted for the Suess effect, the dilution of ^{13}C in the atmosphere by the burning of fossil fuels (Revelle & Suess 1957).

The PDO has historically been the primary indicator of regime shifts in the Bering Sea (Rodionov & Overland 2005), and previously has been related to seabird physiology and diets on the Pribilof Islands (Dorresteijn et al. 2012, Satterthwaite et al. 2012). The PDO is derived from a principal components analysis of sea surface temperature anomalies across the North Pacific (above 20° N Latitude). It is corrected for the global average temperature, so is independent of warming trends associated with climate change (Newman et al. 2016). Positive PDO values are associated with generally warmer conditions (e.g., low winter sea ice extent and early retreat in spring in the Bering Sea), while negative values are associated with generally colder conditions.

In the past few decades, the AO has manifested regime shifts more prominently than the PDO (Rodionov & Overland 2005). The AO is derived from an empirical orthogonal function of monthly mean sea level pressures poleward of 20° N (Thompson & Wallace 1998). Positive AO values are indicative of a polar low pressure system which is associated with a strengthening of the westerly winds circling the arctic and effectively retaining cold air in the northern latitudes. Negative AO values indicate a high pressure system which allows cold arctic air to flow into lower latitudes, cooling North America and Europe, and resulting in warmer winters further north (Tang et al. 2013). The formation, retention, and movement of sea ice are highly influenced by the AO (Rigor et al. 2002).

Another winter phenomenon that potentially affects the productivity of the Bering Sea is the ALow. The ALow (also known as the winter North Pacific Index) is the mean area-weighted sea level pressure in November through March, expressed as anomalies compared to the period 1961-2000. The position and strength of the ALow affects the winter conditions in the Bering Sea, and is hypothesized to affect the degree and depth to which the surface layers are mixed, influencing the nutrients available to organisms during spring and summer plankton production (Rodionov & Overland 2005, Rodionov et al. 2007). ALow potentially affects summer foraging conditions for red-legged kittiwakes and their prey, but has a complex relationship to wintertime storminess (Rodionov et al. 2007), so we included ALow in our primary (but not head) feather models.

Previous research has suggested that red-legged kittiwake migration is influenced by sea ice (Orben et al. 2015), indicates that sea ice during the month of April affects breeding season conditions and reproduction (Murphy et al. 2016, Renner et al. 2016). We would expect, then, that sea ice may explain variability in the fCORT concentrations and stable isotope ratios of head (February sea ice) and primary (April sea ice) feathers. Thus, in our models we used sea ice coverage in February and April as explanatory variables in our head and primary feather models respectively. We calculated Ice Coverage from maps produced by the National Atmospheric and Oceanic Administration (ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/, available from the National Snow and Ice Data Center). We converted images to grayscale in Adobe Photoshop, then calculated the mean pixel intensity, a proxy for ice coverage, in Image J. Based on recent records of red-legged kittiwake winter migration patterns we conservatively calculated sea ice coverage for an area including the Bering Sea, Sea of Okhotsk, and a small portion of the North Pacific (Fig 4.1, R. Orben, unpub. data).

Statistical Analysis

We conducted all analyses in R version 3.2.3 (R Core Development Team). Head fCORT concentrations were calculated by feather length (pg/mm, detrended for the effect of sample mass, Will et al. 2014), and primary fCORT concentrations were calculated by feather sample mass (ng/g). All fCORT concentrations were log-transformed to meet assumptions of normality. We display fCORT anomalies in all figures, calculated as deviations from the long-term mean for each feather type. $\delta^{15}N$ and $\delta^{13}C$ signatures obtained from both head and primary feathers were normally distributed. We normalized and centered the Year and Ice Coverage explanatory variables.

We ran multiple linear regression models using the *lm* function in R to address our study objectives. Models included fCORT, $\delta^{15}N$, or $\delta^{13}C$ as response variables and the aforementioned environmental variables as independent variables. We did not test interaction terms because the biological interpretation of them would be unclear. We used AIC model selection, based on AICc for small sample sizes, to address whether diet and nutritional stress changed in response to changes in the environment. No interaction terms were included in the models. We report the performance of the null model (for illustrative purposes) and all models accounting for 95% of the AIC model weight; an entire set of the candidate models can be found in the Appendix. We modeled response variables at two time scales to accommodate the temporal limitations of some of our explanatory variables: years 1913 – present (hereafter the "century" data set), and 1979 – present (the "forty-year" data set). The century data were tested against the PDO, ALow (primaries only), and Year while the forty-year data were tested against the PDO, ALow (primaries only), Year, AO, and ice cover.

We also used linear regression analysis (*lm* function in R) to test whether the nutritional stress and/or stable isotope signatures in an individual during one season were correlated with stress and stable isotope signatures in that same individual the following season. Finally, we used population data reported by the United States Fish and Wildlife Service's Alaska Maritime National Wildlife Refuge to examine possible relationships between winter physiology/diet and population processes. The red-legged kittiwake population on St. George experienced a strong decline in the years 1976 to 1989, and since has been increasing up to the last reported count in 2014 (Byrd et al. 2008a, Tappa & Romano 2017). We compared fCORT concentrations and stable isotope signatures from the period of population decline (1976-1989) to those from the period of population increase (1990-2014).

Results

Temporal Dynamics of Late Winter Stable Isotopes and Nutritional Stress as Reflected in Head Feathers

In general the PDO best described changes in wintertime $\delta^{15}N$ and $\delta^{13}C$ over the past century (Table 4.1). Year was also a strong predictor, appearing in one of the two best performing models for $\delta^{15}N$ (Table 4.2) and in all of the top performing models for $\delta^{13}C$ (Table 4.3, Fig 4.2). Over the past century it appears that the relationship between red-legged kittiwake's trophic position and environmental conditions may have changed. We found that birds appeared to reverse their response to warm conditions recently. In the past 40 years positive PDO values were associated with depletion in $\delta^{15}N$ signatures (Table 4.2) in contrast to the positive relationship observed over the past century.

Sea ice coverage was positively correlated with $\delta^{15}N$ signatures (Table 4.2), was weakly negatively associated with $\delta^{13}C$ values (Table 4.3), and fCORT concentrations (Table 4.4, Fig 4.3). At the century scale PDO and Year were the best performing variables (Table 4.1), fCORT concentrations have generally declined over time and are lower in years when the PDO is positive (Table 4.4).

Temporal Dynamics of Breeding Season Stable Isotopes and Nutritional Stress as Reflected in Primary Feathers

During the breeding season the trophic level of red-legged kittiwakes has increased over time (Table 4.5). Year accounted for most of the variability in the data (Table 4.6). In the past 40 years sea ice coverage in April and Year were included in all 7 of the top candidate models (Table 4.5). $\delta^{15}N$ was depleted in years of high sea ice coverage and has become more depleted over time (Table 4.5). The variability in $\delta^{13}C$ signatures during the breeding season was best captured by Year (Suess effect, Fig 4.2, Table 4.6) in both the century and 40-year time scale (Table 4.7).

Breeding season fCORT concentrations were best described by the PDO and ALow (Table 4.6). Positive phases of the PDO were associated with low concentrations of fCORT (Table 4.8, Fig 4.4).

Inter-seasonal Relationships

When comparing primary feathers to subsequently grown head feathers (n = 69) we found that elevated stress levels during the breeding season corresponded to elevated stress during the nuptial molt in the following season ($F_{1,67} = 17.26$, $p < 0.0001$, Fig 4.5). $\delta^{13}C$ signatures were positively correlated between the breeding and wintering seasons ($F_{1,67} = 43.12$, $p < 0.0001$, Fig 4.6). There was no correlation in $\delta^{15}N$ signatures between the breeding season and the following winter ($F_{1,67} = 1.675$, $p = 0.2$).

Seven of the museum specimens collected later in the breeding season had already grown new first primary feathers, enabling us to test whether head feather stress and stable isotope values were correlated between the winter period and the following summer period. Diet (as reflected in stable isotope signatures) and nutritional stress during the pre-nuptial molt did not correlate to diet and nutritional stress during the breeding season ($F_{1,6} < 0.733$, $p > 0.425$ for simple linear regressions on $\delta^{15}N$, $\delta^{13}C$, and fCORT, with values for head feathers as the predictor and values for primaries as the response).

Physiology and Population Trends

Head fCORT concentrations were higher ($t_{119} = 5.7484$, $p < 0.0001$) during the period of red-legged kittiwake population decline compared to the period of population increase (Fig 4.7). $\delta^{13}C$ signatures in head feathers from 1976-1989 (mean ± SE: -17.80‰ ± 0.09) were more enriched than those from 1990-2014 (-18.23‰ ± 0.03; $t_{123} = 4.79$, $p < 0.0001$). There was a tendency for $\delta^{15}N$ to be higher after 1989 (15.30‰ ± 0.21 compared to 15.62‰ ± 0.05; $t_{123} = 1.84$, $p = 0.07$).

Discussion

Research in the southeastern Bering Sea has been largely focused on understanding how changes in the region's climate have affected the shelf ecosystem. Here we examined a seabird species, the red-legged kittiwake, which relies primarily on prey from the ocean basin adjacent to the shelf, to better understand what conditions govern summertime food availability. The red-legged kittiwake population on St. George Islands has experienced a marked decline and recovery in its population in the past forty-years. There is evidence that some of this pattern may be attributed to food shortages that occurred during the breeding season. We also investigated whether food shortages persisted and/or occurred in the wintering period. Until recently, technical limitations on our ability to track seabird behavior and physiology outside of the breeding season precluded long-term, year-round studies of seabird responses to environmental conditions.

By collecting feathers grown during the summer (the first primary) and winter (head feathers) we were able to gain insight into what conditions may result in food shortages in the ocean basin on a seasonal and inter-annual basis. During the breeding season red-legged kittiwakes rely on myctophids, primarily *Stenobrachius leucopserus* (Byrd and Williams 1993, Hatch et al. 1993, Kokubun et al. 2015), the most abundant myctophid species in the Bering Sea (Beamish et al. 1999, Moku et al. 2000, Tanimata et al. 2008). We found that during positive phases of the PDO, red-legged kittiwake diets appear to consist of higher trophic level (enriched $\delta^{15}N$) oceanic prey species (depleted $\delta^{13}C$), which corresponds to low fCORT concentrations, suggesting that food may be abundant during these periods. Specific mechanisms of how warm conditions might enhance myctophid abundance and/or availability, which would translate into low nutritional stress incurred by birds, are not well known. One possibility is that red-legged kittiwakes make use of the eddy field (Parades et al. 2014, Yamamoto et al. 2016) located to the south of the Pribilof Islands (Napp et al. 2000). Whether PDO plays any role in determining the intensity of eddy kinetic energy in a given year is not known. Further investigation into what drives myctophid abundance and makes them available to kittiwakes is needed in order to clarify how warm conditions might reduce nutritional stress in breeding red-legged kittiwakes.

In contrast to the breeding period, it is unknown what red-legged kittiwakes eat during the winter. This makes it difficult to interpret the patterns we observed during the non-breeding period. Winters with high sea-ice coverage were associated with higher fCORT concentrations and $\delta^{15}N$ values. This suggests that birds are food limited and may have to rely more heavily on endogenous reserves to meet their energy demands (Hobson 1999, Cherel et al. 2005). The relationship between red-legged kittiwakes and winter sea ice, however, is unclear. Orben et al. (2015) suggested that the foraging of red-legged kittiwakes may be ice associated. It is possible that they may consume hyperiids (Byrd and Williams 1993) during the winter, predatory amphipods that are enriched in $\delta^{15}N$ (Gorbatenko et al. 2014) and are associated with cold waters of the Bering Sea (Pinchuk et al. 2013). However, if they are foraging along the ice edge, fCORT concentrations suggest that too much ice may interfere with their ability to find enough food. Whether or not the enriched $\delta^{15}N$ values are a result of consuming some of their own endogenous reserves (as proposed above) or capturing higher trophic level prey (but not enough of it) during these periods, it is clear high ice coverage in some way compromises the ability of red-legged kittiwakes to get enough food during the winter.

In warm winters with low sea ice coverage red-legged kittiwakes' $\delta^{13}C$ signatures increased. Studies of zooplankton stable isotope signatures indicate that $\delta^{13}C$ values are enriched in the northern and western Bering Sea (Schell et al. 1998, Pomerleau et al. 2014). This suggests that in warm years birds may use shelf-break upwelling areas along the western Bering Sea coast (Schell et al. 1998) or capitalize on tidal currents moving between the north Pacific and Sea of Okhotsk (Kim 2012). Recent overwinter

tracking studies indicate that in the warm winters of 2014- 2015 and 2015-2016 red-legged kittiwakes overwintered primarily along the eastern coast of the Kamchatka peninsula, but also in the Gulf of Anadyr and along the Kuril Islands (R. Orben, unpub data). Warmer conditions with less ice may allow sections of the "Green Belt" (Springer et al. 1996) to persist through the winter, or support areas of upwelling and/or eddies in overwintering areas (Kim 2012, Panteleev et al. 2012). Further investigation into red-legged kittiwake overwinter migration routes, diet composition, and response to sea ice would help to further clarify how sea ice coverage affects non-breeding red-legged kittiwakes and to identify the type of habitat they rely on during the winter.

We found that environmental conditions during the breeding and non-breeding periods, when kittiwakes are in the eastern and western Bering Sea respectively, appear to be correlated. The response of individuals within a year are similar between the two seasons; individuals with high primary (summer) fCORT concentrations had high head (winter) fCORT concentrations (Fig 4.5). These findings are similar to those reported for thick-billed murres, *Uria lomvia,* also breeding in the southeastern Bering Sea (Young et al. 2017). Circulating levels of corticosterone and the ability of birds to mount a response to prolonged stress change in response to both environmental stressors and the demands of different life stages (Sapolsky et al. 2000). The adrenocortical function in kittiwakes is responsive to environmental variability regardless of life stage and can change rapidly, responding to new stress within a matter of days and recovering from natural food shortages within several weeks (Kitaysky et al. 1999, Shultz & Kitaysky 2008, Kitaysky et al. 2010, Schultner et al. 2013a). In our system, seven months separate the growth of the first primary feather and new head feathers. Thus, we submit that the correlation of summer and winter stress is a reflection of environmental conditions that persist throughout the year rather than a carry-over effect. In support of this argument, we also found that $\delta^{13}C$ signatures, which are independent of nutritional stress (Kempster et al. 2007, Williams et al. 2007), were positively correlated between the breeding and wintering periods (Fig 4.6). This suggests that red-legged kittiwakes utilize similar oceanographic habitats governed by the same environmental conditions during the breeding and non-breeding periods.

Our study provides some support for the hypothesis that a reduction in the overwinter survival of adult red-legged kittiwakes contributed to the population decline of this species on St. George. Head fCORT concentrations were significantly higher during the period of population decline compared to the period of growth. This suggests that food shortages during the winter may have resulted in increased levels of stress incurred by birds, which could lead to increased adult mortality or a reduction in the number of birds able to attain reproductive condition and return to the colony to breed. In black-legged kittiwakes (*Rissa tridactyla*) time spent on the wintering grounds was correlated to the ability of individuals to recover from molecular damage that occurred during the breeding season (Schultner et al.

2013b). This suggests that the overwinter period plays an important role in the repair and maintenance at the cellular level. However, to substantiate this hypothesized link between red-legged kittiwake physiological status during molt and survival to the next life stage or skipping reproduction (as both affect adult annual return rates), the relationship between fCORT concentrations and bird survival needs to be investigated on an individual basis.

A Note on Explanatory Variables

While the PDO was a strong predictor of red-legged kittiwake nutritional status and diet over time it is uncertain whether it can be used as a predictor of red-legged kittiwake nutritional status into the future. The PDO did not reflect a climate regime shift that occurred in 1989 and Rodionov and Overland (2005) suggested that perhaps other indices, such as the ALow or AO, may be more illustrative of current climate variability. Schmidt et al. (2015) found that starting in 2007/2008 Brandt's cormorants, *Phalacrocorax penicillatus*, breeding in California broke with a previously established 40-year pattern where El Nino and sea surface temperatures predicted survival and reproduction. It is possible that red-legged kittiwakes will now be faced with novel conditions not seen in the past century, and that the relationships uncovered here may not persist. In our own data we see that, while the PDO corresponds to a clear trend in summer nutritional status, it alone does not capture all of the variability in our data (Fig 4.4). For example, PDO was a top performing variable in our model for $\delta^{15}N$ in primary feathers for the long-term, but not for the near-term data. This discrepancy may be attributed to $\delta^{15}N$ characterizing shifts in the food web (Grecian et al. 2016), a possible signal of ecological regime shifts that occurred independent of changes in the PDO.

Besides the PDO, Year also frequently appeared in the top performing models. The Suess effect accounts for much of the temporal decline in $\delta^{13}C$ signatures in head and primary feathers, however, exactly how much of the decline can be attributed to the anthropogenic burning of fossil fuels is not clear. Correction factors for the Suess effect vary globally and are determined by regional carbon sequestration processes driven by primary producers and ocean physical and biological processes (Gruber et al. 1999, Körtzinger & Quay 2003). An estimate for the Sea of Okhotsk (-0.19 ‰ per year since 1950, Watanabe et al. 2011) accounts for some, but not all, of the strong temporal $\delta^{13}C$ decline observed in our study (year remains a top performing variable in data corrected for the Suess effect, Appendix). We cannot be sure that this correction factor is appropriate to use for the Bering Sea (Gruber et al. 1999, Körtzinger & Quay 2003). Further isotopic analysis of these samples, involving stable isotopes associated with foraging location but free of the Suess effect (e.g., sulphur, Ramos et al. 2011), would differentiate changes in red-legged kittiwake habitat use from changes in the physical environment. Until this analysis is completed we are unable to draw any unequivocal conclusions regarding whether or not red-legged kittiwakes have

experienced shifts in where they obtain their prey. But, while we are unable to precisely correct for the Seuss effect, the depletion in $\delta^{13}C$ signatures in our data set since the 1950's is remarkable. The Bering Sea is remote from any urban centers, yet there is a clear global signal that fossil fuel generated CO_2 has increased in the past century, and evidence that some has been dissolved into this body of water (Revelle and Seuss 1957).

Summary and Conclusions

We found that the PDO was a strong predictor of nutritional stress and trophic level for red-legged kittiwakes throughout the annual cycle, contributing further evidence that regional climate features can be linked to seabird ecology (Sandvik et al. 2005). In long-lived species such as red-legged kittiwakes, examining the response of individuals, rather than population level responses such as reproductive success, may more clearly reveal how the environment influences habitat use and nutritional status. From there, connections may be made to parameters that affect individual fitness and population processes (Satterthwaite et al. 2012). Both stress and stable isotope data indicate that the changes red-legged kittiwakes have experienced in the past century were gradual, occur over several years, and are associated with changes in ocean temperature (PDO) and sea ice dynamics. In general we found that warm winters and breeding season conditions were associated with low levels of nutritional stress incurred by red-legged kittiwakes, which might have facilitated their survival. Warming conditions have been shown to be beneficial to other piscivorous seabirds breeding in North Pacific continental shelf regions that experience winter sea ice cover (Kitaysky & Golubova 2000, Benowitz-Fredericks et al. 2008, Satterthwaite et al. 2012, Harding et al. 2013, Paredes et al. 2014). However, very little is known about the mechanisms that link climate conditions to prey in the Bering Sea basin. Red-legged kittiwakes have already demonstrated that their populations are prone to fluctuating in response to long-term environmental variability. In order to fully understand the response of red-legged kittiwake to future changes we must better understand the migratory patterns of this species, their diet during the non-breeding season, and myctophid ecology.

Acknowledgements

We thank the museum curators and field crews that helped to populate our feather library. These include, but are not limited to: Kimball Garrett, Andrew B. Johnson, Dean Kildaw, Nobuo Kokubun, Rachael Orben, Steve Rogers, Gary Shugart, Alan Springer, Philip Unitt, Jack Withrow, Chris Witt (listed alphabetically). A big thank you to Tim Howe and Norma Haubenstock at the Alaska Stable Isotope Facility. Thank you also to G. Breed and A. Springer whose thoughtful comments gave this manuscript

depth and direction. This project was made possible by the North Pacific Research Board (project # 1410).

References

Alverson DL (1992) A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): The conflict arena. Reviews in Aquatic Sciences 6:203-256

Anonymous (1993) Is it food? Sea Grant, University of Alaska Fairbanks, Fairbanks AK

Aydina K, Mueter F (2007) The Bering Sea—A dynamic food web perspective. Deep-Sea Research II 54:2501–2525

Beamish RJ, Leask KD, Orlov AM, Ivanov OA, Sinclaire B, Balanov AA (1999) The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. Progress in Oceanography 43:399–442

Benowitz-Fredericks ZM, Shultz MT, Kitaysky AS (2008) Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. Deep Sea Research II 55:1868-1876

Benson AJ, Trites AW (2002) Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. Fish and Fisheries 3:95-113

Bond NA, Overland JE, Spillane M, Stabeno P (2003) Recent shifts in the state of the North Pacific. Geophysical Research Letters 30:1-4

Bortolotti GR, Marchant T, Blas J, Cabezas S (2009) Tracking stress: localisation, deposition and stability of corticosterone in feathers. The Journal of Experimental Biology 212:1477-1482

Bortolotti GR, Marchant TA, Blas J, German T (2008) Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. Functional Ecology 22:494-500

Byrd GV, Schmutz JA, Renner HM (2008a) Contrasting population trends of piscivorous seabirds in the Pribilof Islands: A 30-year perspective. Deep Sea Research II 55:1846–1855

Byrd GV, Sydeman WJ, Renner HM, Minobe S (2008b) Responses of piscivorous seabirds at the Pribilof Islands to ocean climate. Deep Sea Research II 55:1856–1867

Byrd GV, Williams JC (1993) Red-legged Kittiake (*Rissa brevirostris*). In: Rodewald PG (ed) The Birds of North America, Cornell Lab of Ornithology, Ithaca, NY

Cherel Y, Hobson KA, Bailleul F, Groscolas R (2005) Nutrition, physiology, and stable isotopes: new information from fasting and molting penguins. Ecology 86:2881-2888

Dorresteijn I, Kitaysky AS, Barger C, Benowitz-Fredericks ZM, Byrd GV, Shultz M, Young R (2012) Climate affects food availability to planktivorous least auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea. Marine Ecology Progress Series 454:207-220

Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography 33:1182-1190

Gorbatenko KM, Lazhentsev AE, Kiyashko SI (2014) Seasonal dynamics of the trophic status of zooplankton in the Sea of Okhotsk (based on data from stable carbon- and nitrogen-isotope analysis). Russian Journal of Marine Biology 40:519-531

Grecian WJ, Taylor GA, Loh G, McGill RAR, Miskelly CM, Phillips RA, Thompson DR, Furness RW (2016) Contrasting migratory responses of two closely related seabirds to long-term climate change. Marine Ecology Progress Series 559:231–242

Gruber N, Keeling CD, Bacastow RB, Guenther PR, Lueker TJ, Wahlen M, Meijer HAJ, Mook WG, Stocke TF (1999) Spatiotemporal patterns of carbon-13 in the global surface oceans and the oceanic Suess effect. Global Biogeochemical Cycles 13:307-335

Harding A, Paredes R, Suryan R, Roby D, Irons D, Orben R, Renner H, Young R, Barger C, Dorresteijn I, Kitaysky A (2013) Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. Deep-Sea Research II 94:178-191

Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103–145

Hatch SA, Byrd, GV, Irons DB, Hunt Jr., GL (1993) Status and ecology of kittiwakes (*Rissa tridactyla* and *R. Brevirostris*) in the North Pacific. In: Vermeer K, Briggs KT, Morgan KH, Siegel-Causey D (eds) Special Publication: The Status, Ecology, and Conservation of Marine Birds of the North Pacific. Canadian Wildlife Service, Environment Canada

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786-798

Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314-326

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series 84:9-18.

Hunt Jr. GL, Coyle KO, Eisner LB, Farley EV, Heintz RA, Mueter F, Napp JM, Overland JE, Ressler PH, Salo S, Stabeno PJ (2011) Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES Journal of Marine Science 68:1230-1243

Hunt Jr. GL, Decker MB, Kitaysky A (1996) Fluctuations in the Bering Sea ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975 to 1991. In: Greenstreet SPR, Tasker ML (eds) Aquatic Predators and their Prey. Fishing News Books

Hunt Jr. GL, Stabeno P, Walters G, Sinclair E, Brodeur RC, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Research II 49:5821-5853

Iverson SJ, Springer AM, Kitaysky AS (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. Marine Ecology Progress Series 352:235-244

Jahncke J, Vlietstra LS, Decker MB, Hunt Jr. GL (2008) Marine bird abundance around the Pribilof Islands: a multi-year comparison. Deep-Sea Research II 55:1809–1826

Kempster B, Zanette L, Longstaffe FJ, MacDougall-Shackleton A, Wingfield JC, Clinchy M (2007) Do stable isotopes reflect nutritional stress? Results from a laboratory experiment on song sparrows. Oecologia 151:365-371

Kim ST (2012) A review of the Sea of Okhotsk ecosystem response to the climate with special emphasis on fish populations. ICES Journal of Marine Science 69:1123–1133

Kitaysky A, Golubova E (2000) Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. Journal of Animal Ecology 69:248-262

Kitaysky A, Kitaiskaia EV, Piatt JF, Wingfield JC (2006) A mechanistic link between chick diet and decline in seabirds? Proceedings of the Royal Society B 273:445-450

Kitaysky AS, Piatt JF, Benowitz-Fredericks ZM, Hatch SA, Shultz MT, Kitaiskaia EV, Wingfield JC (2010) Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Functional Ecology 24:625-637

Kitaysky AS, Piatt JF, Wingfield JC (2007) Stress hormones link food availability and population processes in seabirds. Marine Ecology Progress Series 352:245-258

Kitaysky AS, Wingfield JC, Piatt JF (1999) Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. Functional Ecology 13:577-584

Kokubun N, Yamamoto T, Kikuchi DM, Kitaysky A, Takahashi A (2015) Nocturnal foraging by red-legged kittiwakes, a surface feeding seabird that relies on deep water prey during reproduction. PLoS ONE 10:1-15

Körtzinger A, Quay PD (2003) Relationship between anthropogenic CO_2 and the ^{13}C Suess effect in the North Atlantic Ocean. Global Biogeochemical Cycles 17:1-7

Lattin CR, Reed JM, DesRochers DW, Romero LM (2011) Elevated corticosterone in feathers correlates with corticosterone-induced decreased feather quality: a validation study. Journal of Avian Biology 42:247-252

Litzow MA, Bailey KM, Prahl FG, Heintz R (2006) Climate regime shifts and reorganization of fish communities: the essential fatty acid limitation hypothesis. Marine Ecology Progress Series 315:1-11

Litzow MA, Mueter FJ (2014) Assessing the ecological importance of climate regime shifts: An approach from the North Pacific Ocean. Progress in Oceanography 120:110–119

Mantua NJ, Hare SR (2002) The Pacific Decadal Oscillation. Journal of Oceanography 58:35-44

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069-1079

Moku M, Kawaguchi K, Watanabe H, Ohno A (2000) Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. Marine Ecology Progress Series 207:129–140

Mueter FJ, Broms C, Drinkwater KF, Friedland KD, Hare JA, Hunt Jr. GL, Melle W, Taylor M (2009) Ecosystem responses to recent oceanographic variability in high-latitude Northern Hemisphere ecosystems. Progress in Oceanography 81:93–110

Murphy EC, Roseneau DG, Springer AM, Byrd GV (2016) Breeding chronology and productivity of black-legged kittiwakes *Rissa tridactyla* at Bluff, Alaska, 1975-2008: associations with regional environmental indices and distant colonies. Marine Ornithology 44:183–201

Napp JM, Kendall Jr AW, Schumacker JD (2000) A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Fisheries Oceanography 9:147-162

Newman M, Alexander MA, Ault TR, Cobb KM, Deser C, Di Lorenzo E, Mantua NJ, Miller AJ, Minobe S, Nakamura H, Schneider N, Vimont DJ, Phillips AS, Scott JD, Smith CA (2016) The Pacific Decadal Oscillation, revisited. American Meterological Society 29:4399-4427

Orben RA (unpublished data) Red-legged kittiwake geolocator data. raorben@gmail.com

Orben RA, Irons DB, Paredes R, Roby DD, Phillips RA, Shaffer SA (2015) North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations. Journal of Biogeography 42:401-412

Österblom H, Olsson O, Blenckner T, Furness RW (2008) Junk-food in marine ecosystems. Oikos 117:967-977

Overland JE, Wang M, Wood KR, Percival DB, Bond NA (2012) Recent Bering Sea warm and cold events in a 95-year context. Deep Sea Research Part II: Topical Studies in Oceanography 65-70:6-13

Panteleev G, Nechaev D, Yaremchuk M, Kukuchi T, Luchin V (2012) Variability of the Bering Sea circulation in the period 1992–2010. Journal of Oceanography 68:485–496

Paredes R, Orben RA, Suryan RM, Irons DB, Roby DD, Harding AMA, Young RC, Benoit-Bird K, Ladd C, Renner H, Heppell S, Phillips RA, Kitaysky A (2014) Foraging responses of black-legged kittiwakes to prolonged food shortages around colonies on the Bering Sea shelf. PloS ONE 9:e92520

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320

Pinchuk AI, Coyle KO, Farley EV, Renner HM (2013) Emergence of the Arctic *Themisto libellula* (Amphipoda: Hyperiidae) on the southeastern Bering Sea shelf as a result of the recent cooling, and its potential impact on the pelagic food web. ICES Journal of Marine Science 70:1244-1254

Pomerleau C, Nelson RJ, Hunt BPV, Sastri AR, Williams W (2014) Spatial patterns in zooplankton communities and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) in relation to oceanographic conditions in the sub-Arctic Pacific and western Arctic regions during the summer of 2008. Journal of Plankton Research 36:757-775

R Core Development Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing

Ramos R, Ramírez F, Carrasco JL, Jover L (2011) Insights into the spatiotemporal component of feeding ecology: an isotopic approach for conservation management sciences. Diversity and Distributions 17:338–349

Renner HM, Drummond BA, Benson A-M, Paredes R (2014) Reproductive success of kittiwakes and murres in sequential stages of the nesting period: relationships with diet and oceanography. Deep-Sea Research II 109:251-265

Renner HM, Mueter F, Drummond BA, Warzybok JA, Sinclair EH (2012) Patterns of change in diets of two piscivorous seabird species during 35 years in the Pribilof Islands. Deep Sea Research II 65-70:273–291

Renner M, Salo S, Eisner LB, Ressler PH, Ladd C, Kuletz KJ, Santora JA, Piatt JF, Drew GS, Hunt Jr. GL (2016) Timing of ice retreat alters seabird abundances and distributions in the southeast Bering Sea. Biology Letters 12:20160276

Revelle R, Suess HE (1957) Carbon dioxide exchange between atmosphere and ocean and the question of an increase of atmospheric CO, during the past decades. Tellus IX:18-27

Rigor IG, Wallace JM, Colony RL (2002) Response of sea ice to the Arctic Oscillation. Journal of Climate 15:2648-2663

Rodionov S, Overland JE (2005) Application of a sequential regime shift detection method to the Bering Sea ecosystem. ICES Journal of Marine Science 62:328-332

Rodionov SN, Bond NA, Overland JE (2007) The Aleutian Low, storm tracks, and winter climate variability in the Bering Sea. Deep-Sea Research II 54:2560–2577

Sandvik H, Erikstad KE, Barrett RT, Yoccoz NG (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. Journal of Animal Ecology 74:817–831

Sapolsky RM, Romero LM, Munck AU (2000) How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocrine Reviews 21:55-89

Satterthwaite WH, Hatch SA, Piatt JF, Kitaysky AS, Mangel M (2010) Unifying quantitative life-history theory and field endocrinology to assess prudent parenthood in a long-lived seabird. Evolutionary Ecology Research 12:779–792

Satterthwaite WH, Kitaysky AS, Mangel M (2012) Linking climate variability, productivity and stress to demography in a long-lived seabird. Marine Ecology Progress Series 454:221-235

Schell DM, Barnett BA, Vinette KA (1998) Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. Marine Ecology Progress Series 162:11-23

Schmidt AE, Dybala KE, Botsford LW, Eadie JM, Bradley RW, Jahncke J (2015) Shifting effects of ocean conditions on survival and breeding probability of a long-lived seabird. PloS ONE 10:1-19

Schultner J, Kitaysky AS, Gabrielsen GW, Hatch SA, Bech C (2013a) Differential reproductive responses to stress reveal the role of life-history strategies within a species. Proceedings of the Royal Society B 280:20132090

Schultner J, Moe B, Chastel O, Bech C, Kitaysky AS (2013b) Migration and stress during reproduction govern telomere dynamics in a seabird. Biology Letters 10:20130889

Shultz MT, Kitaysky AS (2008) Spatial and temporal dynamics of corticosterone and corticosterone binding globulin are driven by environmental heterogeneity. General and Comparative Endocrinology 155:717–728

Springer AM (1992) A review: Walleye pollock in the North Pacific-how much difference do they really make? Fisheries Oceanography 1:80-96

Springer AM (1998) Is it all climate change? Why marine bird and mammal populations fluctuate in the North Pacific. In: G. Halloway, P. Muller, and D. Henderson (eds) Biotic impacts of extratropical climate change in the Pacific, Univ. Hawaii:109-119

Springer AM, Byrd GV, Iverson SJ (2007) Hot oceanography: planktivorous seabirds reveal ecosystem responses to warming of the Bering Sea. Marine Ecology Progress Series 352:289-297

Springer AM, McRoy CP, Flint MV (1996) The Bering Sea Green Belt: shelf-edge processes and ecosystem production. Fisheries Oceanography 5:205-223

Springer AM, van Vliet GB (2014) Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. Proceedings of the National Academy of Sciences 111:E1880-E1888

Storer, RW (1987) The possible significance of large eyes in the Red-legged Kittiwake. Condor 89:192-194

Tang Q, Zhang X, Yang X, Francis JA (2013) Cold winter extremes in northern continents linked to Arctic sea ice loss. Environmental Research Letters 8:014036

Tanimata N, Yamamura O, Sakurai Y, Azumaya T (2008) Dietary shift and feeding intensity of *Stenobrachius leucopsarus* in the Bering Sea. Journal ofOceanography 64:185-194

Tappa JD, Romano MD (2017) Biological monitoring at St. George Island, Alaska in 2016. U.S. Fish and Wildlife Service, Alaska Maritime Wildlife Refuge, Homer, AK

Thompson DWJ, Wallace JM (1998) The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. Geophysical Research Letters 25:1297-1300

Watanabe YW, Chiba T, Tanaka T (2011) Recent change in the oceanic uptake rate of anthropogenic carbon in the North Pacific subpolar region determined by using a carbon-13 time series. Journal of Geophysical Research 116:C02006

Will A, Watanuki Y, Kikuchi DM, Sato N, Ito M, Callahan M, Wynne-Edwards K, Hatch S, Elliott K, Slater L, Takahashi A, Kitaysky A (2015) Feather corticosterone reveals stress associated with dietary changes in a breeding seabird. Ecology and Evolution 5:4221-4232

Will AP, Suzuki Y, Elliott KH, Hatch SA, Watanuki Y, Kitaysky AS (2014) Feather corticosterone reveals developmental stress in seabirds. The Journal of Experimental Biology 217:2371-2376

Williams CT, Buck CL, Sears J, Kitaysky AS (2007) Effects of nutritional restriction on nitrogen and carbon stable isotopes in growing seabirds. Oecologia 153:11-18

Wingfield JC, Farner DS (1975) The determination of five steroids in avian plasma by radioimmunoassay and competitive protein-binding. Steroids 26:311-327

Yamamoto T, Kokubun N, Kikuchi DM, Sato N, Takahashi A, Will AP, Kitaysky AS, Watanuki Y (2016) Differential responses of seabirds to environmental variability over 2 years in the continental shelf and oceanic habitats of southeastern Bering Sea. Biogeosciences 13:2405-2414

Young RC, Orben RA, Will AP, Kitaysky AS (2017) Relationship between telomere dynamics and movement and behavior during winter in the thick-billed murre. Marine Ecology Progress Series doi: 10.3354/meps12022

Zador S, Hunt Jr. GL, TenBrink T, Aydin K (2013) Combined seabird indices show lagged relationships between environmental conditions and breeding activity. Marine Ecology Progress Series 485:245–258

Zhang J, Woodgate R, Moritz R (2010) Sea ice response to atmospheric and oceanic forcing in the Bering Sea. Journal of Physical Oceanography 40:1729-1747

Figures

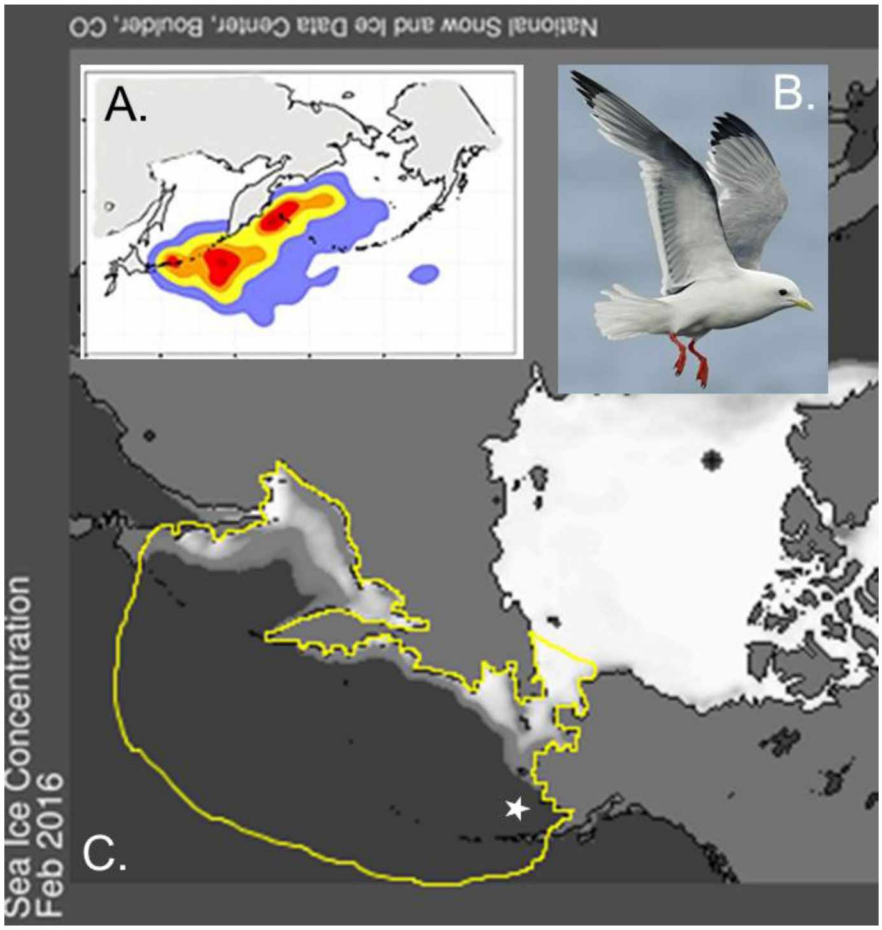

Figure 4.1 Study Area and red-legged kittiwake. A) Map of area used by overwintering red-legged kittiwake in February tracked during the winters of 2011-2012, 2014-2015, and 2015-2016 (courtesy of R. Orben, unpub. data). B) A red-legged kittiwake, photo by Alan Murphy. C) Area used to calculate ice coverage. St. George Island is indicated by the star.

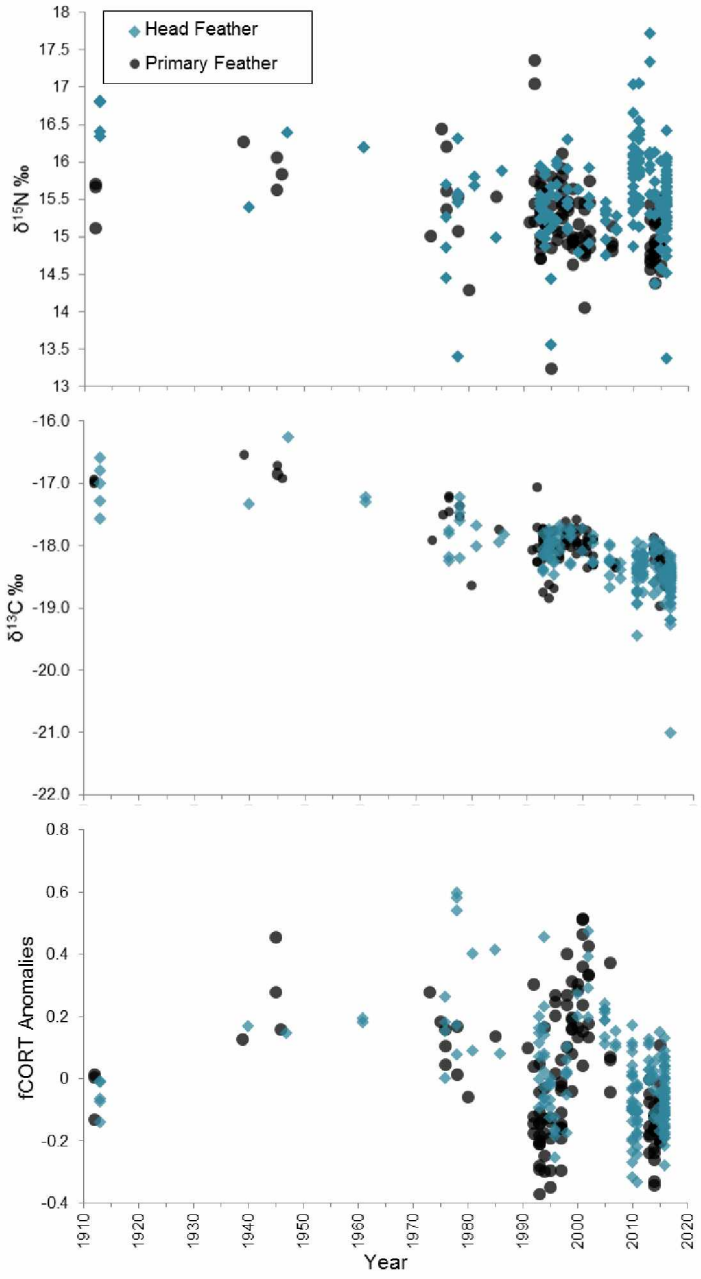

Figure 4.2 Changes in red-legged kittiwake stable isotope signatures and stress exposure from 1913 to the present (2016). A) $\delta^{15}N$ values for head feathers (grey diamonds, n = 194 individuals) and first primaries (black circles, n = 122 individuals). B) $\delta^{13}C$ values for head feathers and first primaries. The decline in $\delta^{13}C$ values due to fossil fuel emissions (the Suess effect) likely accounts for the decline since ~1950; red-legged kittiwakes live far from urban centers and consume primarily mesopelagic prey. C). fCORT concentration anomalies for head feathers and first primaries. Concentrations have been converted to anomalies (concentration – mean concentration) for each feather to illustrate temporal trends and avoid comparing concentrations between feather types.

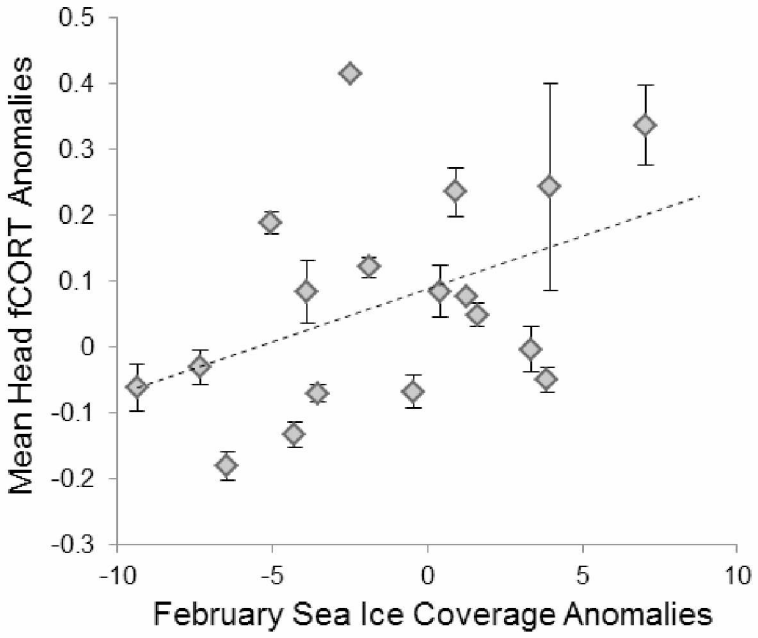

Figure 4.3 Exposure of red-legged kittiwake to stress during the winter (as revealed by head fCORT concentrations) increased during years of high February sea ice coverage. The average of annual head fCORT anomalies are displayed ±SE, n = 18 years; dashed line represents the slope of the linear regression (Table 4.4).

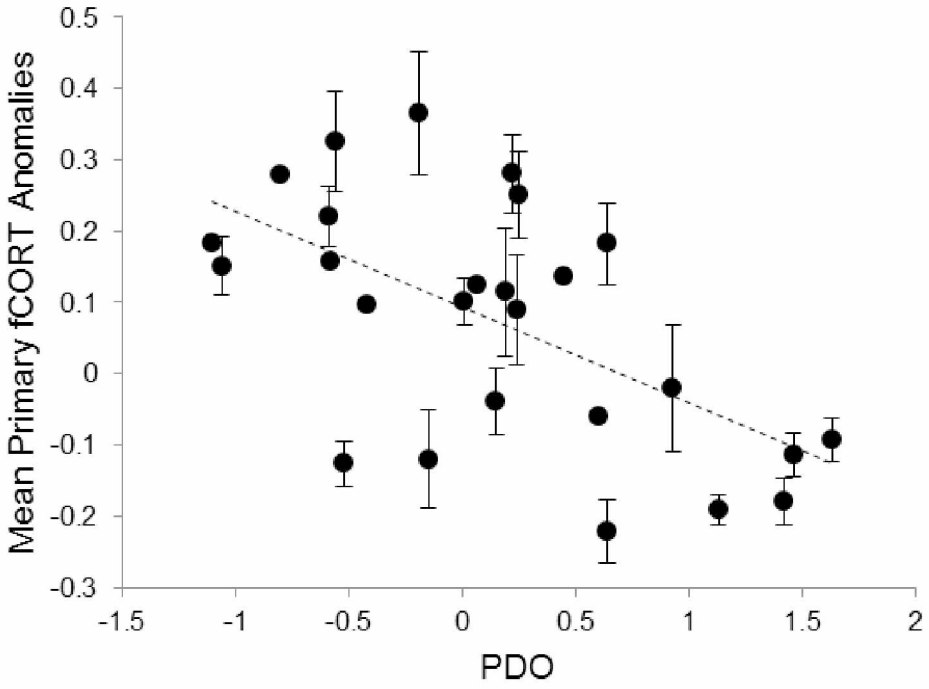

Figure 4.4 Summer stress in red-legged kittiwakes (as reflected in primary fCORT concentrations) was inversely related to PDO. Annual mean primary fCORT anomalies ± SE, n = 27 years; line represents the slope of the linear regression (Table 4.8).

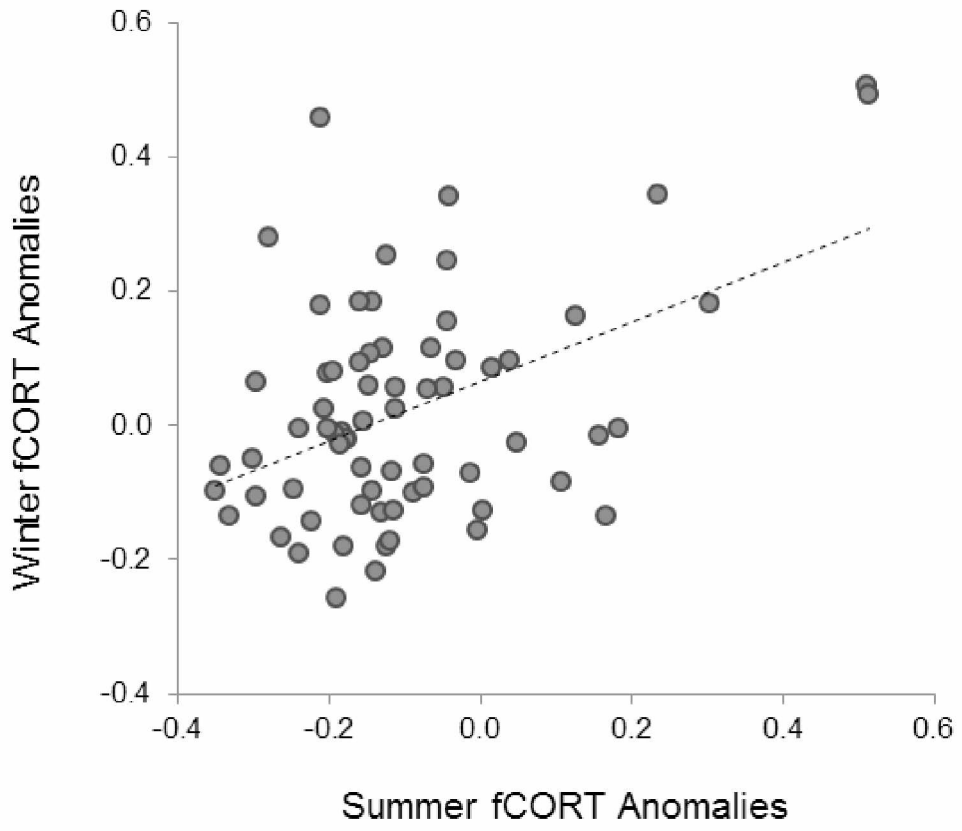

Figure 4.5 Summer and winter stress levels in red-legged kittiwakes were positively correlated. Head and primary fCORT concentrations were analyzed for 69 individuals from 15 different years between 1913 and 2016; dashed line represents the slope of the linear regression ($R^2 = 0.21$).

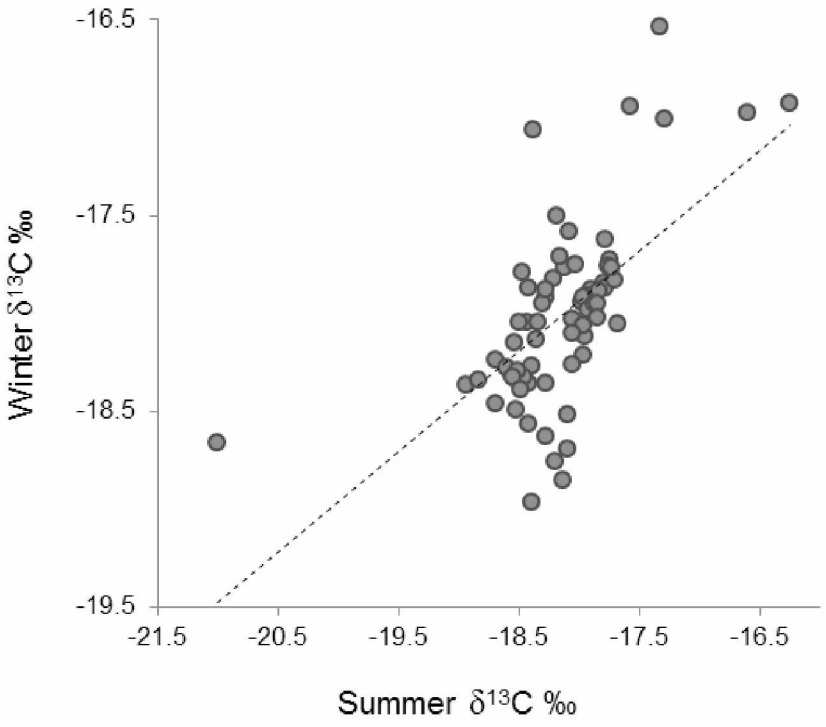

Figure 4.6 $\delta^{13}C$ is positively correlated within individual red-legged kittiwakes between the summer and winter periods, indicating that birds may forage in a particular habitat type independent of geographical location. Both primary and head feathers were analyzed from 69 individuals, sampled from 15 years between 1913 to 2016; dashed line represents the slope of the linear regression ($R^2 = 0.39$).

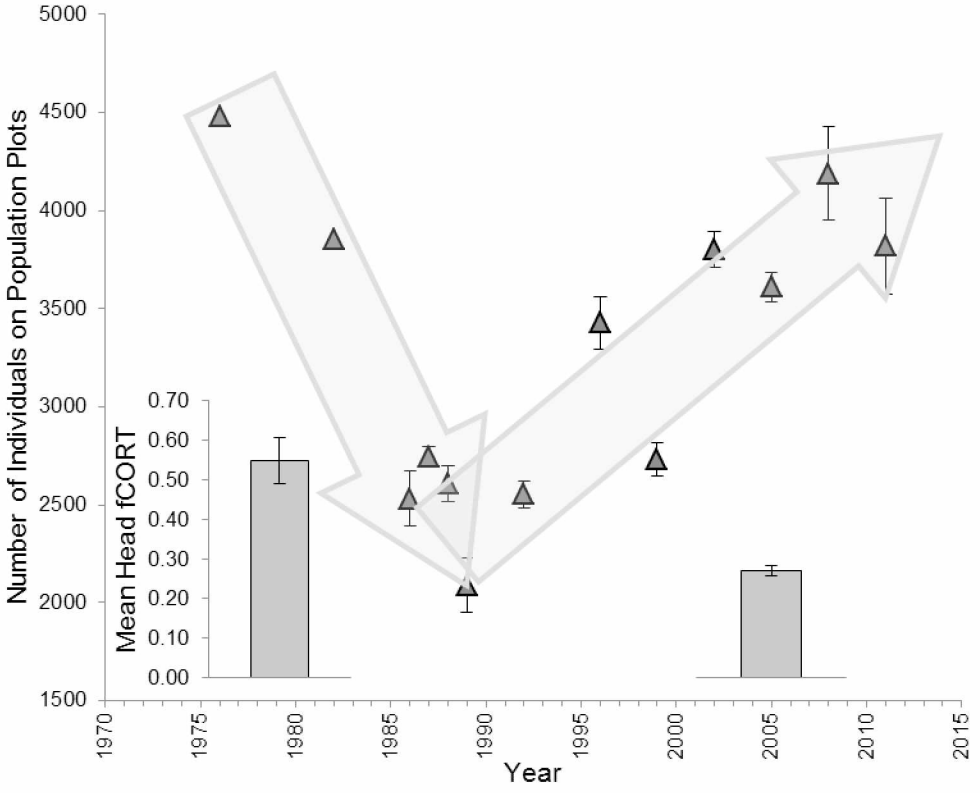

Figure 4.7 Population trajectories and exposure to stress during the winter: red-legged kittiwakes incurred higher levels of stress in winter (as reflected in head feathers) during the period of population decline compared to the period population increase. Population counts (shown are annual mean ± SE) conducted by the USFWS (Tappa & Romano 2017) are presented in tandem with a comparison of head fCORT concentrations from a period when the red-legged kittiwake population was declining (1976-1989) to a period in which it was increasing (1990-2014, indicated by arrows). Overlaid are the mean head fCORT concentrations ± SE for specimens from the same periods (0.55 pg/mm ± 0.06, n = 13, 1976-1989 and = 0.28 pg/mm ± 0.01, n = 112).

Tables

Table 4.1 Summed AIC weights for head feather model parameters. Below are displayed the summed model weights for the variables included in the models to describe head fCORT, $\delta^{15}N$, and $\delta^{13}C$. In the upper panel are the summed AIC weights for the full data set ("Century") and in the lower panel are the summed AIC weights for the forty-year data set. Variables appear in order of rank, with those at the top receiving the most weight.

	fCORT Σ*wi*		δ15N Σ*wi*		δ13C Σ*wi*	
Century	**Year**	0.999	**PDOa**	0.992	**PDOa**	0.980
	PDOa	0.332	**Year**	0.583	**Year**	0.980
Forty-year	**AO**	0.954	**PDOa**	0.948	**PDOa**	0.964
	IceFeb	0.954	**Year**	0.893	**Year**	0.964
	PDOa	0.954	**AO**	0.833	**AO**	0.534
	Year	0.917	**IceFeb**	0.379	**IceFeb**	0.294

Table 4.2 95% confidence set of $\delta^{15}N$ head feather models. Coefficient estimates ± standard error that do not contain zero are italicized.

							Coefficient Estimates				
Century	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**AO**	**IceFeb**
Year+PDOa	0.08	2	194	4	334.96	0.583	*15.363*	*-0.0035*	*-0.1251*	--	--
PDOa	0.07	1	194	3	335.68	0.409	*15.667*	--	*-0.1364*	--	--
Null		1	194	2	346.91	0.001	*15.582*	--	--	--	--
Forty-year	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**AO**	**IceFeb**
Year+AO+PDOa	0.17	3	176	5	261.97	0.449	*15.641*	*0.0119*	*-0.1154*	*-0.0971*	--
Year+PDOa+AO+IceFeb	0.18	4	176	6	262.80	0.297	*15.632*	*0.0145*	*-0.1153*	*-0.0876*	*0.0137*
Year+IceFeb+PDOa	0.16	3	176	5	265.38	0.082	*15.688*	*0.0188*	*-0.1676*	--	*0.0193*
Year+PDOa	0.14	2	176	4	265.83	0.065	*15.709*	*0.0157*	*-0.1760*	--	--
AO+PDOa	0.14	2	176	4	266.18	0.055	*15.581*	--	*-0.0696*	*-0.1299*	--
AO	0.13	1	176	3	267.29	0.032	*15.527*	--	--	*-0.1650*	--
Null		1	176	2	288.90	0.000	*15.563*	--	--	--	--

Table 4.3 95% confidence set of $\delta^{13}C$ head feather models. Coefficient estimates ± standard error that do not contain zero are italicized.

							Coefficient Estimates				
Century	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**AO**	**IceFeb**
Year+PDOa	0.53	2	194	4	130.01	0.980	*-18.334*	*-0.0168*	*-0.0698*	--	--
Null		1	194	2	272.98	0.000	*-18.261*	--	--	--	--
Forty-year	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**AO**	**IceFeb**
Year+AO+PDOa	0.34	3	176	5	99.85	0.383	*-18.325*	*-0.0204*	*-0.0805*	*0.0407*	--
Year+PDOa	0.33	2	176	4	100.42	0.288	*-18.354*	*-0.0220*	*-0.0551*	--	--
Year+PDOa+AO+IceFeb	0.34	4	176	6	101.70	0.152	*-18.323*	*-0.0211*	*-0.0806*	*0.0381*	-0.0038
Year+IceFeb+PDOa	0.33	3	176	5	101.83	0.142	*-18.347*	*-0.0229*	*-0.0578*	--	-0.0062
Null		1	176	2	166.71	0.000	*-18.348*	--	--	--	--

Table 4.4 95% confidence set of fCORT head feather models. Coefficient estimates ± standard error that do not contain zero are italicized.

							Coefficient Estimates				
Century	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**AO**	**IceFeb**
Year	0.08	1	194	3	-168.64	0.667	*0.261*	*-0.0023*	--	--	--
Year+PDOa	0.08	2	194	4	-167.25	0.332	*0.266*	*-0.0022*	-0.0082	--	--
Null		1	194	2	-154.21	0.0005	*0.277*	--	--	--	--
Forty-year	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**AO**	**IceFeb**
Year+PDOa+AO+IceFeb	0.23	4	176	6	-215.80	0.917	*0.256*	*-0.0040*	-0.0104	*0.0346*	*0.0096*
IceFeb+AO+PDOa	0.20	3	176	5	-209.38	0.037	*0.270*	--	*-0.0227*	*0.0462*	*0.0135*
Null		1	176	2	-177.02	0.000	*0.260*	--	--	--	--

Table 4.5 95% confidence set of $\delta^{15}N$ primary feather models. Coefficient estimates ± standard error that do not contain zero are italicized.

							Coefficient Estimates					
Century	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**Alow**	**AO**	**IceApr**
Year+PDOa	0.16	2	122	4	172.64	0.345	*15.151*	*-0.0108*	*0.0919*	--	--	--
Year+PDOa+ALow	0.17	3	122	5	173.39	0.238	*15.161*	*-0.0105*	*0.0803*	*-0.0880*	--	--
Year+ALow	0.16	2	122	4	173.62	0.212	*15.202*	*-0.0096*	--	*-0.1098*	--	--
Year	0.14	1	122	3	173.69	0.205	*15.198*	*-0.0099*	--	--	--	--
Null		1	122	2	190.10	0.000	*15.216*	--	--	--	--	--
Forty-year	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**Alow**	**AO**	**IceApr**
Year+IceA	0.18	2	108	4	142.14	0.242	*15.238*	*-0.0249*	--	--	--	*-0.0369*
Year+Alow+IceA	0.20	3	108	5	142.38	0.214	*15.236*	*-0.0229*	--	*-0.1088*	--	*-0.0361*
Year+PDOa+Alow+AO+IceA	0.22	5	108	7	143.65	0.113	*15.289*	*-0.0240*	*-0.1785*	*-0.1538*	*0.1128*	*-0.0636*
Year+AO+IceA	0.19	3	108	5	143.80	0.105	*15.221*	*-0.0242*	--	--	0.0368	*-0.0361*
Year+PDOa+Alow+IceA	0.20	4	108	6	143.96	0.097	*15.274*	*-0.0241*	-0.0636	*-0.1248*	--	*-0.0468*
Year+Alow+AO+IceA	0.20	4	108	6	144.07	0.092	*15.218*	*-0.0222*	--	*-0.1089*	0.0369	*-0.0353*
Year+PDOa+IceA	0.18	3	108	5	144.11	0.090	*15.257*	*-0.0256*	-0.0308	--	--	*-0.0422*
Null		1	108	2	159.94	0.000	*15.156*	--	--	--	--	--

Table 4.6 Summed AIC weights for primary feather model parameters. Below are displayed the summed model weights for the variables included in the models to describe primary fCORT, $\delta^{15}N$, and $\delta^{13}C$. In the upper panel are the summed AIC weights for the full data set ("Century") and in the lower panel are the summed AIC weights for the forty-year data set. Variables appear in order of rank, with those at the top receiving the most weight.

	fCORT Σwi		δ15N Σwi		δ13C Σwi	
Century	**Alow**	1.000	**Year**	1.000	**Year**	1.000
	PDOa	1.000	**PDOa**	0.583	**PDOa**	0.770
	Year	0.273	**Alow**	0.450	**Alow**	0.455
Forty-year	**Alow**	0.967	**Year**	0.955	**Year**	0.970
	PDOa	0.967	**IceA**	0.955	**PDOa**	0.679
	IceA	0.792	**Alow**	0.517	**Alow**	0.430
	Year	0.564	**AO**	0.311	**IceA**	0.351
	AO	0.405	**PDOa**	0.301	**AO**	0.240

Table 4.7 95% confidence set of $\delta^{13}C$ primary feather models. Coefficient estimates ± standard error that do not contain zero are italicized.

							Coefficient Estimates					
Century	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**Alow**	**AO**	**IceApr**
Year+PDOa	0.58	2	122	4	39.73	0.399	*-17.980*	*-0.0157*	*-0.0611*	--	--	--
Year+PDOa+ALow	0.59	3	122	5	39.87	0.372	*-17.974*	*-0.0155*	*-0.0691*	*-0.0614*	--	--
Year	0.56	1	122	3	41.73	0.146	*-18.011*	*-0.0163*	--	--	--	--
Year+ALow	0.57	2	122	4	42.86	0.083	*-18.009*	*-0.0162*	--	-0.0426	--	--
Null		1	122	2	141.27	0.000	*-17.981*	--	--	--	--	--
Forty-year	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**Alow**	**AO**	**IceApr**
Year+PDOa	0.19	2	108	4	28.37	0.172	*15.157*	*-0.0190*	*0.1229*	--	--	--
Year+PDOa+Alow	0.20	3	108	5	29.07	0.122	*15.161*	*-0.0174*	*0.1115*	*-0.0882*	--	--
Year+PDOa+IceA	0.20	3	108	5	29.25	0.111	*15.257*	*-0.0256*	-0.0308	--	--	*-0.0422*
Year	0.17	1	108	3	29.40	0.103	*15.222*	*-0.0177*	--	--	--	--
Year+PDOa+Alow+IceA	0.21	4	108	6	29.42	0.102	*15.274*	*-0.0241*	-0.0636	*0.1248*	--	*-0.0468*
Year+PDOa+Alow+AO+IceA	0.22	5	108	7	30.23	0.068	*15.289*	*-0.0240*	*-0.1784*	*-0.1538*	*0.1127*	*-0.0214*
Year+PDOa+AO	0.19	3	108	5	30.46	0.061	*15.159*	*-0.0191*	*0.1267*	--	-0.0085	--
Year+Alow	0.17	2	108	4	30.85	0.050	*15.219*	*-0.0157*	--	*-0.1242*	--	--
Year+IceA	0.17	2	108	4	30.98	0.047	*15.238*	*-0.0249*	--	--	--	*-0.0369*
Year+AO	0.17	2	108	4	31.01	0.046	*15.195*	*-0.0169*	--	--	0.0564	--
Year+PDOa+Alow+AO	0.20	4	108	6	31.13	0.043	*15.161*	*-0.0174*	*0.1122*	*-0.0880*	-0.0014	--
Year+Alow+IceA	0.18	3	108	5	32.40	0.023	*15.236*	*-0.0229*	--	*-0.1088*	--	*-0.0361*
Year+Alow+AO	0.17	3	108	5	32.49	0.022	*15.193*	*-0.0148*	--	*-0.1238*	0.0560	--
Null		1	108	2	47.04	0.000	*15.156*	--	--	--	--	--

Table 4.8 95% confidence set of fCORT primary feather models. Coefficient estimates ± standard error that do not contain zero are italicized.

							Coefficient Estimates					
Century	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**Alow**	**AO**	**IceApr**
PDOa+ALow	0.14	2	122	4	-108.60	0.727	*1.454*	--	*-0.1532*	*-0.1567*	--	--
Year+PDOa+ALow	0.49	3	122	5	-106.64	0.273	*1.453*	-0.0003	*-0.1517*	*-0.1555*	--	--
Null		1	122	2	-30.78	9.16E-18	*1.374*	--	--	--	--	--
Forty-year	R^2	k	n	df	AICc	*wi*	**Intercept**	**Year**	**PDOa**	**Alow**	**AO**	**IceApr**
Year+PDOa+Alow+IceA	0.50	4	108	6	-91.26	0.387	*1.482*	-0.0016	*-0.2056*	*-0.1794*	--	*-0.0153*
PDOa+Alow+AO+IceA	0.49	4	108	6	-90.58	0.275	*1.473*	--	*-0.2021*	*-0.1841*	0.0028	*-0.0135*
Year+PDOa+Alow+AO+IceA	0.50	5	108	7	-89.07	0.130	*1.482*	-0.0016	*-0.2082*	*-0.1801*	0.0026	*-0.0156*
PDOa+Alow	0.47	2	108	4	-89.05	0.128	*1.447*	--	*-0.1476*	*-0.1650*	--	--
Year+PDOa+Alow	0.47	3	108	5	-87.03	0.047	*1.445*	0.0006	*-0.1484*	*-0.1675*	--	--
Null		1	108	2.00	-25.24	1.79E-15	*1.357*	--	--	--	--	--

Appendix 4.A: Museum Specimens and Supplemental Information

Museum Specimens

Table 4.A-1 Number of samples collected by year. Table 4.A-1 A lists primary feather samples, Table 4.A-1B lists head feather samples.

A.

Year	Sample Number
1912	3
1939	1
1945	2
1946	1
1973	1
1975	1
1976	3
1978	2
1980	1
1985	1
1991	1
1992	5
1993	12
1994	6
1995	5
1996	4
1997	11
1998	4
1999	7
2000	4
2001	7
2002	5
2006	4
2013	7
2014	14
2015	10

B.

Year	Sample Number
1913	5
1940	1
1947	1
1961	2
1976	4
1978	5
1981	2
1985	1
1986	1
1993	7
1994	11
1995	7
1996	5
1998	7
2000	2
2002	4
2005	8
2007	3
2010	24
2011	18
2013	9
2014	7
2015	9
2016	51

Table 4.A-2 Red-legged kittiwakes sampled from museum collections. ID# = the collection number. Museum acronyms: CM = Carnegie Museum of Natural History, LACM = Natural History Museum of Los Angeles County, MSB = Museum of Southwestern Biology, PSM= James R. Slater Museum, SDNHM = San Diego Natural History Museum, and UAM = University of Alaska Fairbanks' Museum of the North. "Y" indicates the feather type (first primary or head) was available for that particular specimen, "N" indicates that it was not.

ID#	Source	First Primary	Head
49292	CM	Y	Y
49293	CM	N	Y
49294	CM	Y	Y
49290	CM	Y	Y
49291	CM	N	Y
90372	LACM	N	Y
90371	LACM	N	Y
90380	LACM	Y	Y
90379	LACM	Y	Y
90378	LACM	N	Y
96970	LACM	N	Y
96955	LACM	N	Y
23362	MSB	Y	N
1439	PSM	Y	N
1440	PSM	Y	N
21596	SDNHM	Y	Y
40286	SDNHM	Y	Y
43425	SDNHM	Y	Y
40285	SDNHM	Y	Y
19282	SDNHM	Y	Y
43426	SDNHM	Y	Y
2380	UAM	N	Y
2344	UAM	N	Y
4925	UAM	Y	Y
5363	UAM	Y	Y
13157	UAM	Y	Y
15035	UAM	N	Y
20204	UAM	Y	Y
20206	UAM	Y	Y
20207	UAM	Y	Y
20205	UAM	Y	Y
26857	UAM	Y	Y
26848	UAM	Y	Y
26852	UAM	Y	Y

ID#	Source	First Primary	Head
26849	UAM	Y	Y
20004	UAM	Y	N
20037	UAM	Y	N
28926	UAM	Y	N
26852	UAM	Y	N
26857	UAM	Y	N
2900	UAM	Y	N
10218	UAM	Y	N
10222	UAM	Y	N
10224	UAM	Y	N
10221	UAM	Y	N
28915	UAM	Y	N
28923	UAM	Y	N
28925	UAM	Y	N
19999	UAM	Y	N
19896	UAM	Y	N
20035	UAM	Y	N
19931	UAM	Y	N
19897	UAM	Y	N
19904	UAM	Y	N
19927	UAM	Y	N
19900	UAM	Y	N
19901	UAM	Y	N
19925	UAM	Y	N
15462	UAM	Y	N
13144	UAM	Y	N
14771	UAM	Y	N
13743	UAM	Y	N
14776	UAM	Y	N
14062	UAM	Y	N
13746	UAM	Y	N
13443	UAM	Y	N
14773	UAM	Y	N

Stable Isotope Standards

Table 4.A-3 Inter-lab comparison of internal standards. We ran pugel, the internal standard used at the University of California Santa Cruz's (UCSC) stable isotope facility, at the University of Alaska Fairbanks' Alaska Stable Isotope Facility (ASIF). We report the mean stable isotope ratios (ASIF n = 13, UCSC n = 16) from each facility as well as the standard deviation.

ASIF			
$\delta^{15}N$	SD	$\delta^{13}C$	SD
5.39	0.07	-12.56	0.21

UCSC			
$\delta^{15}N$	SD	$\delta^{13}C$	SD
5.38	0.09	-12.61	0.16

Candidate Models

Table 4.A-4 Candidate models for head fCORT.

Century	AIC Model Selection						Coefficient Estimate				
Models	**df**	**k**	**n**	**AICc**	**ΔAICc**	**AICc weight**	**Intercept**	**Year**	**PDOa**	**AO**	**IceFeb**
Year	3	1	194	-168.640	0.000	0.667	4.942	-0.002	--	--	--
Year+PDOa	4	2	194	-167.249	1.391	0.332	4.779	-0.002	-0.008	--	--
PDOa	3	1	194	-154.406	14.235	0.001	0.286	--	-0.016	--	--
intercept	2	1	194	-154.192	14.448	0.000	0.277	--	--	--	--
Forty-year											
Year+PDOa+AO+IceFeb	6	4	176	-215.802	0.000	0.917	7.403	-0.004	-0.010	0.035	0.010
IceFeb+AO+PDOa	5	3	176	-209.376	6.427	0.037	-0.866	--	-0.023	0.046	0.014
Year+AO+PDOa	5	3	176	-208.781	7.022	0.027	11.753	-0.006	--	0.028	-0.010
Year+IceFeb+PDOa	5	3	176	-207.061	8.742	0.012	10.978	-0.006	0.010	--	0.007
Year	3	1	176	-205.203	10.600	0.005	13.384	-0.007	--	--	--
Year+PDOa	4	2	176	-203.731	12.072	0.002	13.939	-0.007	0.007	--	--
IceFeb	3	1	176	-192.577	23.225	0.000	-0.820	--	--	--	0.013
AO+PDOa	4	2	176	-190.780	25.022	0.000	0.291	--	-0.032	0.044	--
IceFeb+PDOa	4	2	176	-190.547	25.255	0.000	-0.829	--	0.001	--	0.013
AO	3	1	176	-183.818	31.984	0.000	0.266	--	--	0.027	--
intercept	2	1	176	-177.021	38.781	0.000	0.260	--	--	--	--
PDOa	3	1	176	-175.941	39.861	0.000	0.266	--	-0.009	--	--

Table 4.A-5 Candidate models for head $\delta^{15}N$.

	AIC Model Selection						Coefficient Estimate				
Century	df	k	n	AICc	ΔAICc	AICc weight	Intercept	Year	PDOa	AO	IceFeb
Year+PDOa	4	2	194	334.965	0.000	0.583	22.608	-0.003	-0.125	--	--
PDOa	3	1	194	335.677	0.712	0.409	15.667	--	-0.136	--	--
Year	3	1	194	343.899	8.934	0.007	25.086	-0.005	--	--	--
intercept	2	1	194	346.907	11.942	0.001	15.582	--	--	--	--
Forty-year											
Year+AO+PDOa	5	3	176	261.974	0.000	0.449	-8.348	0.012	-0.115	-0.097	--
Year+PDOa+AO+IceFeb	6	4	176	262.802	0.828	0.297	-14.591	0.014	-0.115	-0.088	0.014
Year+IceFeb+PDOa	5	3	176	265.377	3.404	0.082	-23.652	0.019	-0.168	--	0.019
Year+PDOa	4	2	176	265.833	3.859	0.065	-15.933	0.016	-0.176	--	--
AO+PDOa	4	2	176	266.177	4.203	0.055	15.581	--	-0.070	-0.130	--
AO	3	1	176	267.288	5.314	0.032	15.527	--	--	-0.165	--
IceFeb+AO+PDOa	5	3	176	268.242	6.268	0.020	15.650	--	-0.070	-0.130	-0.001
PDOa	3	1	176	275.434	13.461	0.001	15.655	--	-0.139	--	--
IceFeb+PDOa	4	2	176	277.469	15.495	0.000	15.547	--	-0.138	--	0.001
Year	3	1	176	287.350	25.376	0.000	-1.986	0.009	--	--	--
intercept	2	1	176	288.899	26.925	0.000	15.563	--	--	--	--
IceFeb	3	1	176	289.657	27.683	0.000	14.459	--	--	--	0.013

Table 4.A-6 Candidate models for head $\delta^{13}C$

	AIC Model Selection						Coefficient Estimate				
Century	df	k	n	AICc	ΔAICc	AICc weight	Intercept	Year	PDOa	AO	IceFeb
Year+PDOa	4	2	194	130.011	0.000	0.980	15.387	-0.017	-0.070	--	--
Year	3	1	194	137.819	7.808	0.020	16.770	-0.017	--	--	--
PDOa	3	1	194	258.731	128.720	0.000	-18.183	-0.124	--	--	--
intercept	2	1	194	272.979	142.968	0.000	-18.261	--	--	--	--
Forty-year											
Year+AO+PDOa	5	3	176	99.849	0.000	0.383	22.605	-0.020	-0.081	0.041	--
Year+PDOa	4	2	176	100.422	0.573	0.288	25.786	-0.022	-0.055	--	--
Year+PDOa+AO+IceFeb	6	4	176	101.702	1.853	0.152	24.328	-0.021	-0.081	0.038	-0.004
Year+IceFeb+PDOa	5	3	176	101.828	1.978	0.142	28.267	-0.023	-0.058	--	-0.006
Year	3	1	176	104.598	4.748	0.036	30.155	-0.024	--	--	--
IceFeb+AO+PDOa	5	3	176	136.275	36.426	0.000	-19.708	--	-0.146	0.100	0.017
AO+PDOa	4	2	176	139.206	39.356	0.000	-18.222	-0.159	0.097	--	--
IceFeb+PDOa	4	2	176	148.198	48.349	0.000	-19.629	--	-0.094	--	0.016
PDOa	3	1	176	149.988	50.138	0.000	-18.277	--	-0.107	--	--
IceFeb	3	1	176	160.152	60.302	0.000	-20.376	--	--	--	0.024
intercept	2	1	176	166.712	66.863	0.000	-18.348	--	--	--	--
AO	3	1	176	168.258	68.408	0.000	-18.345	--	--	0.017	--

Table 4.A-7 Candidate models for primary fCORT.

	AIC Model Selection						Coefficient Estimate					
Century	df	k	n	AICc	ΔAICc	AICc weight	Intercept	Year	PDOa	Alow	AO	IceApr
PDOa+ALow	4	2	122	-108.600	0.000	0.727	1.454	--	-0.153	-0.157	--	--
Year+PDOa+ALow	5	3	122	-106.641	1.959	0.273	1.997	0.000	-0.152	-0.155	--	--
PDOa	3	1	122	-73.356	35.244	0.000	1.439	--	-0.136	--	--	--
Year+PDOa	4	2	122	-72.491	36.109	0.000	3.251	-0.001	-0.131	--	--	--
Year+ALow	4	2	122	-45.296	63.304	0.000	5.146	-0.002	--	-0.114	--	--
ALow	3	1	122	-43.083	65.517	0.000	1.378	--	--	-0.120	--	--
Year	3	1	122	-34.049	74.551	0.000	5.779	-0.002	--	--	--	--
intercept	2	1	122	-30.775	77.825	0.000	1.374	--	--	--	--	--
Forty-year												
Year+PDOa+Alow+IceA	6	4	108	-91.260	0.000	0.387	5.947	-0.002	-0.206	-0.179	--	-0.015
PDOa+Alow+AO+IceA	6	4	108	-90.576	0.685	0.275	2.566	--	-0.202	-0.184	0.003	-0.013
Year+PDOa+Alow+AO+IceA	7	5	108	-89.072	2.189	0.130	5.975	-0.002	-0.208	-0.180	0.003	-0.016
PDOa+Alow	4	2	108	-89.051	2.209	0.128	1.447	--	-0.148	-0.165	--	--
Year+PDOa+Alow	5	3	108	-87.035	4.226	0.047	0.314	0.001	-0.148	-0.167	--	--
Year+PDOa+Alow+AO	6	4	108	-86.328	4.933	0.033	1.448	0.000	-0.137	-0.164	-0.026	--
Alow+AO+IceA	5	3	108	-66.052	25.208	0.000	0.023	--	--	-0.126	-0.087	0.017
Year+Alow+AO+IceA	6	4	108	-63.943	27.317	0.000	-0.956	0.000	--	-0.128	-0.086	0.017
PDOa	3	1	108	-58.659	32.601	0.000	1.429	--	-0.129	--	--	--
Year+PDOa+AO	5	3	108	-58.503	32.757	0.000	7.806	-0.003	-0.110	--	-0.039	--
PDOa+AO	4	2	108	-58.149	33.112	0.000	1.434	--	-0.117	--	-0.030	--
Year+PDOa	4	2	108	-58.069	33.191	0.000	6.279	-0.002	-0.127	--	--	--
Year+PDOa+IceA	5	3	108	-57.512	33.749	0.000	9.724	-0.004	-0.158	--	--	-0.009
PDOa+IceA	4	2	108	-56.826	34.434	0.000	1.681	--	-0.141	--	--	-0.003
PDOa+AO+IceA	5	3	108	-56.072	35.189	0.000	1.316	--	-0.110	--	-0.033	0.001
Alow+IceA	4	2	108	-51.193	40.067	0.000	-0.063	--	--	-0.120	--	0.018
AO+IceA	4	2	108	-50.971	40.289	0.000	-0.050	--	--	--	-0.083	0.018
Year+Alow+IceA	5	3	108	-49.961	41.300	0.000	-4.487	0.002	--	-0.128	--	0.019
Year+Alow+AO	5	3	108	-49.767	41.493	0.000	7.716	-0.003	--	-0.120	-0.095	--
PDOa+Alow+AO	5	3	108	-49.767	41.493	0.000	7.716	-0.003	--	-0.120	-0.095	--
Alow+AO	4	2	108	-49.699	41.561	0.000	1.399	--	--	-0.132	-0.090	--
Year+AO+IceA	5	3	108	-49.521	41.739	0.000	3.746	-0.002	--	--	-0.086	0.016
IceA	3	1	108	-39.695	51.565	0.000	-0.128	--	--	--	--	0.018
Year+AO	4	2	108	-38.957	52.303	0.000	11.683	-0.005	--	--	-0.095	--
Year+IceA	4	2	108	-37.623	53.637	0.000	0.216	0.000	--	--	--	0.018
Alow	3	1	108	-36.191	55.069	0.000	1.362	--	--	-0.126	--	--
AO	3	1	108	-35.623	55.638	0.000	1.392	--	--	--	-0.086	--
Year+Alow	4	2	108	-34.686	56.574	0.000	4.803	-0.002	--	-0.120	--	--
Year	3	1	108	-25.773	65.487	0.000	8.760	-0.004	--	--	--	--
intercept	2	1	108	-25.240	66.020	0.000	1.357	--	--	--	--	--

Table 4.A-8 Candidate models for primary $\delta^{13}C$.

	AIC Model Selection						Coefficient Estimate					
Century	df	k	n	AIC	ΔAIC	AICc weight	Intercept	Year	PDOa	Alow	AO	IceApr
Year+PDOa	4	2	122	39.728	0.000	0.399	13.431	-0.016	-0.061	--	--	--
Year+PDOa+ALow	5	3	122	39.867	0.140	0.372	12.936	-0.015	-0.069	-0.061	--	--
Year	3	1	122	41.733	2.005	0.146	14.606	-0.016	--	--	--	--
Year+ALow	4	2	122	42.855	3.127	0.083	14.370	-0.016	--	-0.043	--	--
PDOa+ALow	4	2	122	130.626	90.898	0.000	-17.899	--	-0.157	-0.131	--	--
PDOa	3	1	122	132.802	93.075	0.000	17.912	--	-0.143	--	--	--
ALow	3	1	122	141.234	101.506	0.000	-17.977	--	--	-0.094	--	--
intercept	2	1	122	141.266	101.538	0.000	-17.981	--	--	--	--	--
Forty-year												
Year+PDOa	4	2	108	28.375	0.000	0.172	8.592	-0.013	-0.053	--	--	--
Year+PDOa+Alow	5	3	108	29.068	0.693	0.122	6.556	-0.012	-0.060	-0.057	--	--
Year+PDOa+IceA	5	3	108	29.252	0.877	0.111	13.179	-0.015	-0.095	--	--	-0.012
Year	3	1	108	29.397	1.022	0.103	9.624	-0.014	--	--	--	--
Year+PDOa+Alow+IceA	6	4	108	29.416	1.041	0.102	11.744	-0.014	-0.113	-0.068	--	-0.014
Year+PDOa+Alow+AO+IceA	7	5	108	30.230	1.855	0.068	12.271	-0.014	-0.163	-0.081	0.050	-0.021
Year+PDOa+AO	5	3	108	30.462	2.087	0.061	8.345	-0.013	-0.056	--	0.006	--
Year+Alow	4	2	108	30.846	2.472	0.050	8.374	-0.013	--	-0.038	--	--
Year+IceA	4	2	108	30.983	2.608	0.047	7.488	-0.013	--	--	--	0.005
Year+AO	4	2	108	31.007	2.632	0.046	10.306	-0.014	--	--	-0.022	--
Year+PDOa+Alow+AO	6	4	108	31.134	2.759	0.043	6.067	-0.012	-0.065	-0.059	0.011	--
Year+Alow+IceA	5	3	108	32.400	4.025	0.023	6.021	-0.012	--	-0.040	--	0.005
Year+Alow+AO	5	3	108	32.488	4.113	0.022	9.055	-0.014	--	-0.038	-0.022	--
Year+AO+IceA	5	3	108	32.725	4.350	0.020	8.305	-0.013	--	--	-0.020	0.004
Year+Alow+AO+IceA	6	4	108	34.182	5.807	0.009	6.839	-0.013	--	-0.040	-0.020	0.004
PDOa+Alow	4	2	108	42.021	13.646	0.000	-18.039	--	-0.079	-0.111	--	--
PDOa+Alow+AO	5	3	108	42.618	14.244	0.000	-18.046	--	-0.098	-0.113	0.046	--
Alow+IceA	4	2	108	42.989	14.615	0.000	-19.230	--	--	-0.085	--	0.014
AO+IceA	4	2	108	42.989	14.615	0.000	-19.230	--	--	-0.085	--	0.014
IceA	3	1	108	43.907	15.532	0.000	-19.277	--	--	--	--	0.015
PDOa+Alow+AO+IceA	6	4	108	44.738	16.364	0.000	-17.852	--	-0.110	-0.116	0.051	-0.002
PDOa	3	1	108	44.898	16.523	0.000	-18.050	--	-0.066	--	--	--
Alow+AO+IceA	5	3	108	45.100	16.725	0.000	-19.233	--	--	-0.085	0.003	0.014
PDOa+AO	4	2	108	45.702	17.327	0.000	-18.058	--	-0.085	--	0.043	--
PDOa+IceA	4	2	108	45.739	17.364	0.000	-18.963	--	-0.024	--	--	0.011
Alow	3	1	108	45.814	17.439	0.000	-18.084	--	--	-0.090	--	--
intercept	2	1	108	47.043	18.669	0.000	-18.088	--	--	--	--	--
PDOa+AO+IceA	5	3	108	47.448	19.073	0.000	-18.642	--	-0.052	--	0.029	0.007
Alow+AO	4	2	108	47.890	19.516	0.000	-18.080	--	--	-0.090	0.000	--
AO	3	1	108	49.038	20.663	0.000	-18.089	--	--	--	0.003	--

Table 4.A-9 Candidate models for primary $\delta^{15}N$.

	AIC Model Selection						Coefficient Estimate					
Century	df	k	n	AIC	ΔAIC	AICc weight	Intercept	Year	PDOa	Alow	AO	IceApr
Year+PDOa	4	2	122	172.645	0.000	0.345	36.808	-0.011	0.092	--	--	--
Year+PDOa+ALow	5	3	122	173.392	0.747	0.238	36.098	-0.010	0.080	-0.088	--	--
Year+ALow	4	2	122	173.619	0.974	0.212	34.430	-0.010	--	-0.110	--	--
Year	3	1	122	173.691	1.046	0.205	35.039	-0.010	--	--	--	--
ALow	3	1	122	189.058	16.413	0.000	15.222	--	--	-0.140	--	--
intercept	2	1	122	190.103	17.458	0.000	15.216	--	--	--	--	--
PDOa+ALow	4	2	122	190.984	18.339	0.000	15.211	--	0.021	-0.135	--	--
PDOa	3	1	122	191.684	19.039	0.000	15.199	--	0.036	--	--	--
Forty-year												
Year+IceA	4	2	108	142.136	0.000	0.242	67.988	-0.025	--	--	--	
Year+Alow+IceA	5	3	108	142.379	0.243	0.214	63.983	-0.023	--	-0.109	--	-0.037
Year+PDOa+Alow+AO+IceA	7	5	108	143.654	1.518	0.113	68.411	-0.024	-0.178	-0.154	0.113	-0.036
Year+AO+IceA	5	3	108	143.798	1.661	0.105	66.480	-0.024	--	--	0.037	-0.064
Year+PDOa+Alow+IceA	6	4	108	143.958	1.822	0.097	67.211	-0.024	-0.064	-0.125	--	-0.036
Year+Alow+AO+IceA	6	4	108	144.072	1.935	0.092	62.470	-0.022	--	-0.109	0.037	-0.047
Year+PDOa+IceA	5	3	108	144.110	1.974	0.090	69.838	-0.026	-0.031	--	--	-0.035
Year+PDOa	4	2	108	147.583	5.447	0.016	53.090	-0.019	0.123	--	--	-0.042
Year+PDOa+Alow	5	3	108	148.578	6.442	0.010	49.949	-0.017	0.112	-0.088	--	--
Year+PDOa+AO	5	3	108	149.681	7.545	0.006	53.425	-0.019	0.127	--	-0.008	--
Year+PDOa+Alow+AO	6	4	108	150.735	8.599	0.003	50.011	-0.017	0.112	-0.088	-0.001	--
Year+Alow	4	2	108	150.884	8.748	0.003	46.576	-0.016	--	-0.124	--	--
Year	3	1	108	151.024	8.887	0.003	50.685	-0.018	--	--	--	--
Year+Alow+AO	5	3	108	152.015	9.879	0.002	44.868	-0.015	--	-0.124	0.056	--
Year+AO	4	2	108	152.119	9.983	0.002	48.949	-0.017	--	--	0.056	--
Alow+IceA	4	2	108	156.135	13.999	0.000	16.669	--	--	-0.193	--	--
Alow+AO+IceA	5	3	108	156.448	14.312	0.000	16.594	--	--	-0.188	0.077	-0.019
PDOa+Alow	4	2	108	156.690	14.553	0.000	15.114	--	0.085	-0.164	--	-0.018
Alow	3	1	108	157.050	14.913	0.000	15.163	--	--	-0.186	--	--
Alow+AO	4	2	108	157.197	15.061	0.000	15.130	--	--	-0.181	0.080	--
PDOa+Alow+AO+IceA	6	4	108	158.027	15.890	0.000	17.708	--	-0.089	-0.213	0.116	--
PDOa+Alow+AO	5	3	108	158.203	16.067	0.000	15.106	--	0.064	-0.166	0.050	-0.031
PDOa	3	1	108	158.394	16.258	0.000	15.097	--	0.104	--	--	--
IceA	3	1	108	159.439	17.302	0.000	16.564	--	--	--	--	--
AO+IceA	4	2	108	159.496	17.360	0.000	16.486	--	--	--	0.083	-0.017
AO	3	1	108	159.808	17.671	0.000	15.121	--	--	--	0.086	-0.017
intercept	2	1	108	159.939	17.803	0.000	15.156	--	--	--	--	--
PDOa+AO	4	2	108	159.985	17.848	0.000	15.090	--	0.084	--	0.045	--
PDOa+IceA	4	2	108	160.414	18.277	0.000	15.429	--	0.088	--	--	--
PDOa+AO+IceA	5	3	108	161.586	19.449	0.000	16.259	--	0.018	--	0.075	-0.004

Analysis with Corrected $\delta^{13}C$ Values

Table 4.A-10 Results of model selection for head $\delta^{13}C$ corrected for Suess effect.

Century	df	k	n	AICc	ΔAICc	AICc weight
PDOa	3	1	194	119.68633	0.000	0.690
Year+PDOa	4	2	194	121.54303	1.857	0.273
intercept	2	1	194	126.43663	6.750	0.024
Year	3	1	194	127.53763	7.851	0.014
Forty-year						
AO+PDOa	4	2	176	98.491924	0.000	0.325
PDOa	3	1	176	99.985099	1.493	0.154
Year+AO+PDOa	5	3	176	100.35451	1.863	0.128
IceFeb+AO+PDOa	5	3	176	100.49679	2.005	0.119
Year+PDOa	4	2	176	100.94528	2.453	0.095
IceFeb+PDOa	4	2	176	101.90635	3.414	0.059
Year+PDOa+AO+IceFeb	6	4	176	102.1982	3.706	0.051
Year+IceFeb+PDOa	5	3	176	102.33417	3.842	0.048
Year	3	1	176	105.15368	6.662	0.012
intercept	2	1	176	106.64759	8.156	0.006
IceFeb	3	1	176	108.46099	9.969	0.002
AO	3	1	176	108.64414	10.152	0.002

Table 4.A-11 Results of model selection for primary $\delta^{13}C$ corrected for Suess effect.

Century	df	k	n	AICc	ΔAIC	AIC weight
PDOa	3	1	122	31.397	0.000	0.387
intercept	2	1	122	32.422	1.025	0.232
PDOa+ALow	4	2	122	32.765	1.367	0.195
Year+PDOa	4	2	122	33.252	1.854	0.153
ALow	3	1	122	34.135	2.738	0.099
Year	3	1	122	34.419	3.022	0.085
Year+PDOa+ALow	5	3	122	34.528	3.130	0.081
Year+ALow	4	2	122	36.192	4.794	0.035
Forty-year						
Year+PDOa	4	2	108	28.555	0.000	0.105
PDOa+IceA	4	2	108	28.756	0.201	0.095
Year+PDOa+Alow	5	3	108	29.213	0.658	0.076
Year+PDOa+IceA	5	3	108	29.486	0.930	0.066
Year	3	1	108	29.583	1.028	0.063
Year+PDOa+Alow+IceA	6	4	108	29.620	1.065	0.062
PDOa+AO+IceA	5	3	108	30.163	1.608	0.047
PDOa	3	1	108	30.190	1.635	0.047
PDOa+Alow+AO+IceA	6	4	108	30.315	1.760	0.044
Year+PDOa+Alow+AO+IceA	7	5	108	30.457	1.902	0.041
intercept	2	1	108	30.593	2.038	0.038
Year+PDOa+AO	5	3	108	30.641	2.086	0.037
Year+Alow	4	2	108	31.010	2.455	0.031
Year+IceA	4	2	108	31.146	2.591	0.029
Year+AO	4	2	108	31.194	2.639	0.028
Year+PDOa+Alow+AO	6	4	108	31.277	2.722	0.027
AO	3	1	108	31.698	3.143	0.022
PDOa+Alow	4	2	108	31.902	3.346	0.020
PDOa+AO	4	2	108	32.186	3.631	0.017
Alow	3	1	108	32.487	3.932	0.015
Year+Alow+IceA	5	3	108	32.538	3.983	0.014
IceA	3	1	108	32.593	4.038	0.014
Year+Alow+AO	5	3	108	32.653	4.097	0.014
Year+AO+IceA	5	3	108	32.891	4.336	0.012
Alow+AO	4	2	108	33.637	5.081	0.008
AO+IceA	4	2	108	33.772	5.217	0.008
PDOa+Alow+AO	5	3	108	33.949	5.394	0.007
Year+Alow+AO+IceA	6	4	108	34.323	5.768	0.006
Alow+IceA	4	2	108	34.563	6.008	0.005
Alow+AO+IceA	5	3	108	35.748	7.193	0.003

General Conclusion

In this dissertation I used seabirds to examine how long-lived species cope with variability in their environment. First, I validated a new technique to detect nutritional stress in seabirds over longer time periods (weeks instead of days) and during times of the year when seabirds are not always accessible to sample (primarily the non-breeding period). I then applied this technique on a short time scale to determine how a single species, throughout its range, copes with changes in diet composition. Linking diet composition and environmental variability has proven somewhat challenging, so I also examined whether characterizing how a seabird group's isotopic niche under different environmental conditions might be used to understand foraging responses. Finally, I brought these tools together to examine how a single species has responded to changes over multiple decades. Here I highlight some of the key findings of this body of work and propose some possible next steps.

The bulk of my work built off of validating that the avian stress hormone (corticosterone) deposited in feathers (fCORT) can be used to detect exposure to nutritional stress in seabirds. This included the experimental work presented in Chapter 1, but also some molecular work, a piece of which is included in the Appendix of Chapter 2. These validations, however, may be more difficult to generalize to other systems than one might hope. Work done in tandem with my own showed that captive Caspian tern (*Hydroprogne caspia*) chicks raised on control and restricted diets reflected the opposite pattern of fCORT deposition as the rhinoceros auklet chicks in Chapter 1: tern chicks raised on a control diet had higher concentrations of fCORT compared to chicks raised on a restricted diet (Patterson et al. 2014). It is, therefore, still necessary for researchers to validate the use of fCORT in their study species in order to correctly interpret the source of the stress recorded in feathers and the direction of the signal.

In Chapter 4 I capitalized on the two molts a kittiwake undergoes during the year in order to characterize their response to conditions during the breeding and non-breeding period. Primary feathers and head feathers are, however, quite different in morphology and it is unclear how best to compare feathers with different structures. Here I chose to compare them using their hormone concentration per unit mass of feather, and even then did not risk making any statements about whether birds were more or less stressed in one season or another. In order to fully capitalize on this tool to measure stress during different periods of the year we must first determine how to compare those feathers. One way to find out would be to analyze the feathers of individuals with a known nutritional history that was held constant for the growth of all feather types. Currently we are working with collaborators at the University of Calgary to address this issue. Our colleagues will use high-performance liquid chromatography tandem mass spectrometry to measure the concentration of the actual CORT molecule in different feather types sampled from the same rhinoceros auklet chicks featured in Chapter 1 so that we can establish a method of comparing conditions birds experience during different parts of the year.

One of the major objectives of this dissertation was to use samples collected over multiple decades to examine how long-lived organisms are affected by changes in their environment. In Chapter 3 I addressed the issue of detecting an environmental signal in the foraging habits of a group of seabirds that breed in an environment which varies inter-annually. I demonstrated that characterizing the isotopic niche of that seabird group provided new insight into how species partition food resources during food-limiting conditions, and also the role that habitat heterogeneity plays in the way in which food resources are partitioned. On a colony where seabirds had access to multiple habitat types, their isotopic niche contracted during food limitation in contrast to seabirds breeding on a colony with access to a single type of habitat, where the isotopic niche expanded. Seabirds are not the only species that are central place foragers, or that are centrally located in areas with more or less habitat heterogeneity. An expansion of the isotopic niche during food-abundant periods has also been observed to occur in wolves inhabiting a diverse habitat (Darimont et al. 2009). Whether this pattern of partitioning resources occurs at smaller scales (in small mammals or insects) would need to be tested in order for the conclusions drawn here to gain credibility as a broader pattern of foraging behavior.

Chapters 3 and 4 both focus on the response to long-term environmental change of primarily fish-eating birds breeding on the Pribilof Islands in the Bering Sea. In both cases the results suggest that warmer conditions provide better foraging conditions for murres and kittiwakes. While there was some pre-existing evidence that this may be the case for species relying on the continental shelf of the Bering Sea for foraging during reproduction (Benowitz-Fredericks et al. 2008, Satterthwaite et al. 2012, Harding et al. 2013, Paredes et al. 2014), there was less, but suggestive, evidence that red-legged kittiwakes were affected by environmental conditions in the ocean basin (Springer 1998). As I mentioned in Chapter 3, it is unclear whether a warming Bering Sea would in fact be beneficial for these species. There has yet to be detected any long-term warming trend in the region (Brown et al. 2011), and it may be that the system currently relies on short-term oscillations between cold and warm conditions. For example, abundant young-of-the-year pollock are produced in warm years, but it has been proposed that colder conditions are necessary in order for these young fish to recruit to the population (e.g., Mueter et al. 2011). The seabird community on the Pribilof Islands also reflects a reliance on cold and warm conditions. In contrast to the murres and kittiwakes, planktivorous seabirds, such as least auklets (*Aethia pusilla*), have been shown to thrive under cold, but not warm, conditions (Springer et al. 2007, Benowitz-Fredericks et al. 2008, Dorresteijn et al. 2012). This indicates that the system currently simultaneously supports species that prefer either warm or cold conditions, but not necessarily both, which makes it difficult to predict how indefinite warming may affect the system.

Finally, I combined the use of fCORT and stable isotope analysis to track how a single species, the red-legged kittiwake, has responded to environmental change over multiple decades (Chapter 4).

During the breeding season, and perhaps at times during the non-breeding season, red-legged kittiwakes rely on an abundant mesopelagic forage fish (myctophids) which is a key part of the food web in the Bering Sea basin. I found that warmer conditions (characterized by positive phases of the Pacific Decadal Oscillation and low February sea ice coverage) during both the breeding and non-breeding periods corresponded to lower nutritional stress. It is unclear, however, whether these warm conditions are also beneficial to their prey, or if it simply facilitates the availability of prey to surface-feeding kittiwakes. Chapter 4 highlights how little we know about the ecology of the Bering Sea basin. Without knowing what affects myctophid abundance and availability, or even what red-legged kittiwakes eat during the non-breeding period, it is difficult to understand the mechanisms that drive the patterns we found in the long-term data.

In regards to how long-lived seabirds cope with variability in their environment, I found that they do so in a number of different ways. In Chapter 2 I examined whether and how changes in diet composition affect seabirds and their offspring, and if changes occur, which of the two bears the cost. Both showed signs of nutritional stress during a year when meal deliveries were low in energy content. While changes in adult foraging behavior were documented, they appeared to occur independently of changes in caloric content of the diets they provided for their offspring, suggesting that foraging effort was dictated primarily by prey type. On the Pribilof Islands seabirds shifted their isotopic niche in response to changes in prey availability, presumably focusing on habitat characteristics that yield prey rather than focusing on a specific prey type. These findings indicate that long-lived seabirds adapt their foraging behavior to minimize the costs incurred during food-limiting conditions, and provide a further understanding of what seabirds may be indicating about the environment they inhabit. These studies indicate that by tracking the nutritional status of rhinoceros auklet fledglings (single feather per bird) or the isotopic niche used by murres and kittiwakes (blood sample taken in conjunction with other work) we could continue to document changes in prey composition and availability more directly in the Gulf of Alaska and Bering Sea than may be possible through the lens of seabird breeding performance.

References

Benowitz-Fredericks ZM, Shultz MT, Kitaysky AS. (2008). Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. *Deep Sea Research II.* 55:1868-1876.

Brown ZW, van Dijken GL, Arrigo KR. (2011). A reassessment of primary production and environmental change in the Bering Sea. *Journal of Geophysical Research*. 116: C08014.

Darimont CT, Paquet PC, Reimchen TE. (2009). Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *Journal of Animal Ecology*. 78:126-133.

Dorresteijn I, Kitaysky AS, Barger C, Benowitz-Fredericks ZM, Byrd GV, Shultz M, Young R. (2012). Climate affects food availability to planktivorous least auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea. *Marine Ecology Progress Series.* 454:207-220.

Harding A, Paredes R, Suryan R, Roby D, Irons D, Orben R, Renner H, Young R, Barger C, Dorresteijn I, Kitaysky A (2013) Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. *Deep-Sea Research II.* 94:178-191.

Mueter FJ, Bond NA, Ianelli JN, Hollowed AB. (2011). Expected declines in recruitment of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea under future climate change. *ICES Journal of Marine Science*. 68:1284-1296

Paredes R, Orben RA, Suryan RM, Irons DB, Roby DD, Harding AMA, Young RC, Benoit-Bird K, Ladd C, Renner H, Heppell S, Phillips RA, Kitaysky A. (2014). Foraging responses of black-legged kittiwakes to prolonged food shortages around colonies on the Bering Sea shelf. *PloS ONE.* 9:e92520.

Patterson AGL, Kitaysky AS, Lyons DE, Roby DD. (2014). Nutritional stress affects corticosterone deposition in feathers of Caspian tern chicks. *Journal of Avian Biology.* 46 :18-24.

Satterthwaite WH, Kitaysky AS, Mangel M. (2012). Linking climate variability, productivity and stress to demography in a long-lived seabird. *Marine Ecology Progress Series.* 454:221-235.

Springer AM. (1998). Is it all climate change? Why marine bird and mammal populations fluctuate in the North Pacific. In: G. Halloway, P. Muller, and D. Henderson (eds) *Biotic impacts of extratropical climate change in the Pacific*. University of Hawaii:109-119

Springer AM, Byrd GV, Iverson SJ. (2007). Hot oceanography: planktivorous seabirds reveal ecosystem responses to warming of the Bering Sea. *Marine Ecology Progress Series.* 352:289-297

Appendices: IACUC Approval Letters

UNIVERSITY OF ALASKA FAIRBANKS

(907) 474-7800
(907) 474-5638 fax
fyiacuc@uaf.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

October 31, 2011

To: Christine Hunter
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [251294-2] Foraging ecology and survival of rhinoceros auklets

The IACUC reviewed and approved the Amendment/Modification referenced below by Designated Member Review.

Received:	October 26, 2011
Approval Date:	October 31, 2011
Initial Approval Date:	October 31, 2011
Expiration Date:	October 31, 2012

This action is included on the October 31, 2011 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

UNIVERSITY OF ALASKA FAIRBANKS

(907) 474-7800
(907) 474-5638 fax
fyiacuc@uaf.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 3, 2012

To: Alexander Kitaysky
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [251294-7] Foraging ecology and survival of rhinoceros auklets

The IACUC reviewed and approved the Revision to the Personnel List referenced above by Designated Member Review.

Received:	July 2, 2012
Approval Date:	July 3, 2012
Initial Approval Date:	October 31, 2011
Expiration Date:	October 31, 2012

This action is included on the July 26, 2012 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

The PI is responsible for ensuring animal research personnel are aware of the reporting procedures on the following page.

(907) 474-7800
(907) 474-5993 fax
fyiacuc@uaf.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 17, 2013

To: Alexander Kitaysky
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [251294-9] Foraging ecology and survival of rhinoceros auklets

The IACUC reviewed and approved the Amendment/Modification to the Protocol referenced above by Designated Member Review.

Received:	May 15, 2013
Approval Date:	May 17, 2013
Initial Approval Date:	October 31, 2011
Expiration Date:	October 31, 2013

This action is included on the May 29, 2013 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

(907) 474-7800
(907) 474-5993 fax
uaf-iacuc@alaska.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 27, 2014

To: Alexander Kitaysky
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [251294-11] Foraging ecology and survival of rhinoceros auklets

The IACUC reviewed and approved the Amendment/Modification to the Protocol referenced above by Designated Member Review.

Received:	May 12, 2014
Approval Date:	May 27, 2014
Initial Approval Date:	October 31, 2011
Expiration Date:	October 31, 2014

This action is included on the June 12, 2014 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*